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2016–2018 Spread of H5N8 highly pathogenic avian influenza (HPAI) in sub-Saharan Africa: epidemiological and ecological observations

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Background

During the northern hemisphere autumn and winter of 2016–2017, an Asian-origin H5N8 highly pathogenic avian influenza (HPAI) virus of the H5 Goose/Guangdong/96 lineage [Gs/GD/96] clade 2.3.4.4 group B,¹ spread extensively throughout western Eurasia, the Middle East and caused sporadic outbreaks in India and Nepal (Sims *et al.*, 2017). These viruses were found to be genetically closely related to the ancestral isolates at Lake Ubsu-Nur in the Republic of Tyva, in the Russian Federation bordering Mongolia, which have so far not demonstrated the ability to affect humans. During the

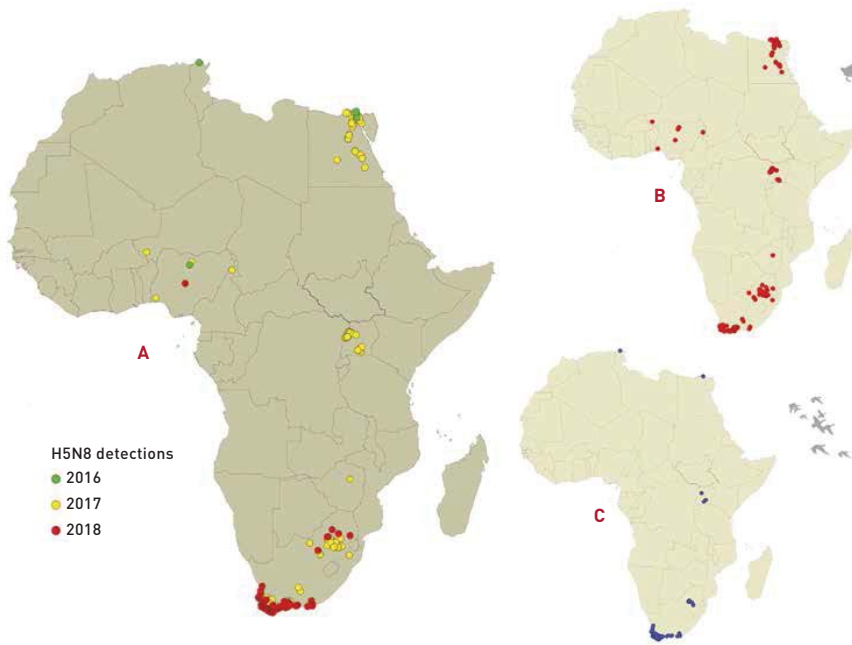
peak of the most extensive HPAI epidemic ever documented, H5N8 dispersed exceptionally widely throughout the Afro-Eurasian waterbird flyway system and, as had been anticipated (Sims and Brown, 2016; FAO, 2016), eventually reached the African continent (Figure 1). In November 2016 Egypt and Tunisia both reported their first detection of the H5N8 HPAI virus, followed in January 2017 by Nigeria, Niger, Cameroon and Uganda (Sims *et al.*, 2017; FAO, 2017). From previous events in 2014–2015 involving another similar H5N8 HPAIV strain, there is sufficient evidence that the transcontinental spread of H5N8 HPAI was due to seasonal migration of wild aquatic birds, mainly that of Palearctic dabbling ducks (Global Consortium for H5N8 and Related Influenza Viruses, 2016; Van den Brand *et al.*, 2018).

Following the first ever recorded incursion of HPAI in Eastern Africa, a series of

¹ For Goose/Guangdong/96-lineage [Gs/GD/96 lineage] H5 clade nomenclature, please see Smith and Donis, 2015 and Li *et al.*, 2017.

Figure 1

Distribution of H5N8 HPAI clade 2.3.4.4 virus detections in Africa (November 2016 to 31 May 2018)



(A) by year of detection; (B) in domestic poultry and captive avian species; (C) in wild birds.

Source: WAHIS, OIE

H5N8 HPAI outbreaks² in April 2017 was also recorded in the north-eastern part of the Democratic Republic of the Congo (OIE, 2018a). Up to this point, spread of the virus could have been explained by the seasonal influx of Palearctic waterfowl and spillover of viruses from overwintering ducks to communities of Afro-tropical aquatic birds and/or poultry as has simultaneously happened in Europe (Napp *et al.*, 2018).

In 2006–2015 such incursion patterns, generally associated with the epidemiological situation in Europe and often involving multiple independent introduction events by closely related viruses, were observed with H5N1 HPAI viruses in West Africa in 2006–2008 and 2014–2015. Sporadic virus introductions were

followed by extended periods of endemicity in poultry (e.g. 2006–2008 and 2014–2017 in Nigeria) and the spread of the virus across international borders through poultry trade (Ekong *et al.*, 2018).

In this context, the arrival of the novel H5N8 HPAI virus in Egypt and sub-Saharan Africa in 2016/2017 raised concerns regarding its potential to become established and disperse further within the affected countries and regions in a manner similar to that of previous Asian H5 HPAI Gs/GD/96 lineage viruses (FAO, 2016; Sims *et al.*, 2017; FAO, 2017). Indeed, further developments in Western Eurasia demonstrated that localized “pockets” of H5N8 infection remained active throughout the spring, summer and autumn of 2017 in northern Italy and Iran, exhibiting patterns that are unusual for this part of the world, since it typically experiences HPAI epidemics in winter or early spring.

Consistent with the growing understanding of the increased capacity of the novel H5N8 HPAI to persist beyond the “usual” seasonal avian influenza activity period, the Democratic

Republic of the Congo reported an accelerating H5N8 HPAI epidemic in poultry in April–June 2017. In May, for the first time in the history of avian influenza (AI) observation, Zimbabwe reported an Asian H5 HPAI Gs/GD/96 lineage, clade 2.3.4.4 AI virus (AIV) in southern areas of the Rift Valley (Figure 1). In June 2017, the virus was also detected in South Africa, where the situation developed into a large-scale epidemic, peaking at the end of the southern winter and the beginning of spring (September–October 2017). Multiple domestic, captive and wild bird species were affected in both the north and the south of the country. The western Cape Province appears to be the most heavily affected region in South Africa to date.

The H5N8 HPAI incursion into South Africa and its extensive geographical spread have resulted in unprecedented losses to the poultry industry. In spite of the lack of recent notifications from the rest of Africa, the situation in other countries of the southern African region could be evolving in a similar direction, being unnoticed by many veterinary services for a variety of reasons: insufficient resources, low accessibility, under reporting, etc. Developments of this kind were long forecasted (Cumming *et al.*, 2008; Mundava *et al.*, 2016), but it is only now that the true scale of consequences related to the ongoing spread of the exotic H5N8 HPAI virus can be evaluated based on information provided by African countries.

By the end of May 2018, there were 285 reports of H5N8 HPAI in Africa (Figures 1 and 2; further details below). Although the end of spring and arrival of summer in the southern hemisphere did seem to bring down the number of poultry outbreaks in South Africa, the virus still continues to circulate in the Western Cape, North West and Gauteng Provinces. From December 2017 to April 2018 the virus spread widely into marine bird populations along the southern coast. The most recent reappearance of the virus in poultry in the north of the country in February–April 2018, after several months’ absence, is also of concern.

The situation is particularly worrying in light of the approaching colder and drier autumn and winter in the coming months, when climatic conditions will favour virus survival in the environment. This may facilitate further

² The term “outbreak” refers to a group of birds, sometimes comprising different species, in a specified geographical location (e.g. farm, village, beach, etc.) confirmed to be affected by H5N8 HPAI. Data used in this analysis were extracted from the World Animal Health Information System (WAHIS) by the World Organisation for Animal Health (OIE), accessed 31 May 2018.

flare-ups of the disease in South Africa and possibly elsewhere. This could lead to the establishment and year-round circulation of H5N8 HPAI in the communities of wild Afro-tropical aquatic birds, as well as in poultry production systems. The disease may become a long-term threat to the poultry industry and subsistence poultry farming in the region. Spread of the virus to highly susceptible species of wild African birds, particularly those with high conservation status, is another serious concern, as it could destroy decades of efforts to protect these birds or even bring some of them to the verge of extinction.

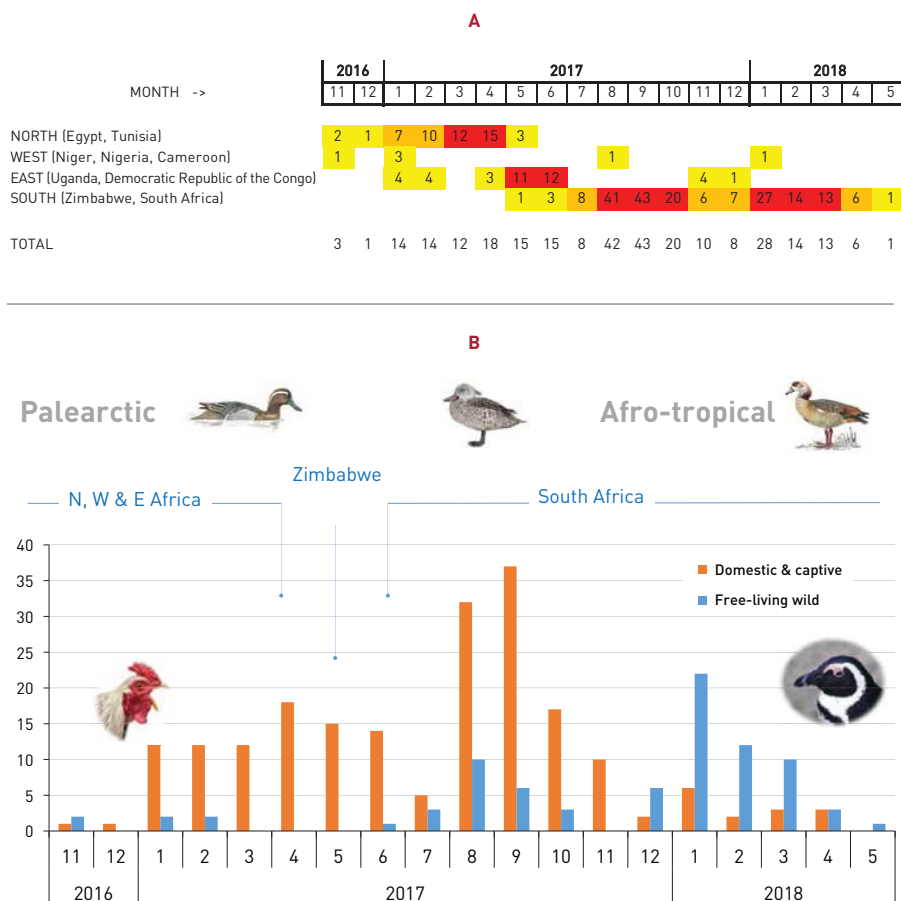
This document builds on a series of FAO EMPRES publications (FAO 2016; Sims et al., 2017) aiming at rapid re-analysis of available information and brief prospective assessment of the ongoing panzootic of the Asian-origin H5 HPAI viruses of the Goose/Guangdong/96 lineage, this time with a focus on Africa. ●

Evolution of the H5N8 HPAI epidemic in Africa (November 2016–May 2018)

In North Africa H5N8 incursions resulted in extended spread of the virus in Egypt (but seemingly not in Tunisia), including many localities of the Upper Nile (Figure 1). The epidemic apparently originated in the north of the country, where large-scale wild bird trapping and hunting are common practice in winter (Selim *et al.*, 2017), as in many other Mediterranean countries where up to two million waterbirds alone are estimated to be harvested annually (Brochet *et al.*, 2016). In fact, H5N8 was detected in wild waterfowl in the north of Egypt, such as in carcasses of common coots (*Fulica atra*) in a fish market in Damietta Governorate on 24 November 2016 and common teals (*Anas crecca*) at a live bird market located in Port Said City on 8 December 2016 (Kandeil *et al.*, 2017; in *Anas crecca*, not *Anas carolinensis* - as was erroneously indicated). From November 2016 to May 2017, a total of 49 outbreaks were reported with the majority associated with domestic species (ducks – 51 percent, chickens – 27 percent, geese – six percent), the remainder being multiple or unidentified species holdings. The epidemic peaked in March–April 2017, generally following the same winter-spring

Figure 2

Evolution of the H5N8 HPAI clade 2.3.4.4 epidemic in Africa in 2016–2018 (as of 31 May 2018)



A. Monthly disease timelines represented as virus detections pooled by four regions of Africa (yellow: five or less detections; orange: six–ten detections; red: 11 or more detections).

B. Epicurve of total reported monthly H5N8 HPAI outbreaks (including domestic, captive and collections; orange bars) and cases in free-ranging wild birds (blue bars) and geographic progression of the disease (see blue line on top).

Source: WAHIS, OIE

activity pattern observed with the previous Gs/GD/96-lineage H5N1 HPAI viruses.

At least four distinct H5N8 HPAI Group B clade 2.3.4.4 reassortant viruses from Europe and Asia were introduced into Egypt and subsequently isolated from poultry (Salaheldin *et al.*, 2018), which may suggest repeated introduction of the subtype with overwintering waterfowl, who may have acted as the original source of the epidemic, similar to the situation in 2016–2017 in Europe (Napp *et al.*, 2018). However, a general lack of sequence data prevents conclusive analysis. The current H5N8 HPAI status in Egypt is suspected

to be endemic throughout the country (FAO Emergency Centre for Transboundary Animal Diseases – ECTAD Egypt, personal communication), although no official reports have been submitted to OIE since May 2017.

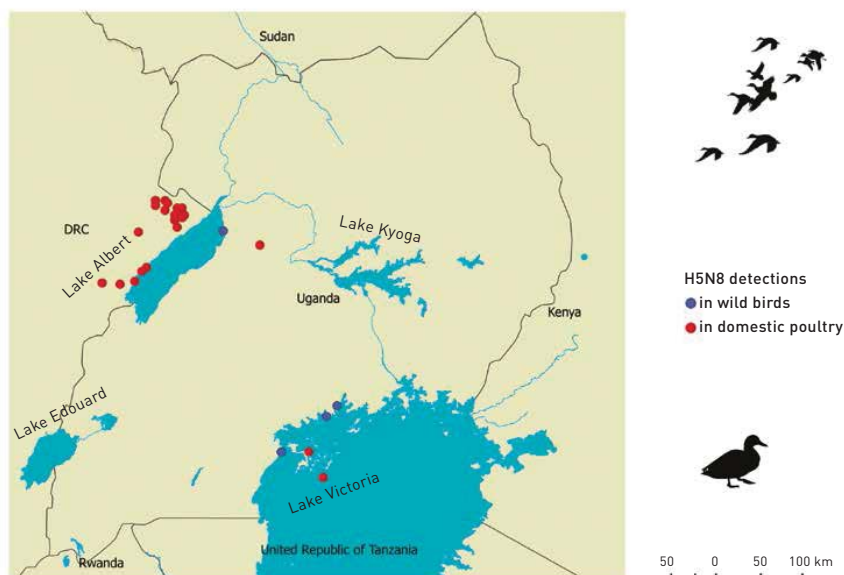
Western Africa There have been few reports of H5N8 in western Africa (n=6; Figures 1 and 2a) and all have originated from domestic poultry: they include chickens, ducks and Indian peafowl (*Pavo cristatus*). The scarcity of observations and their broad timespan (November 2016–January 2017; August 2017 and January 2018), suggest the low sensitivity

of the surveillance system in place. Thus, continuous circulation of the virus cannot be ruled out, e.g. in farms and live bird markets with low biosecurity standards, at least in Nigeria (Wade *et al.*, 2018). An alternative explanation may be that the most recent outbreak detected in Nigeria in January 2018 was due to novel introduction of the same virus with overwintering Palearctic anatids. Several extensive freshwater wetlands in the country, such as Hadejia-Nguru Wetland and Lake Chad, provide opportunities for interaction with overwintering ducks through hunting, trapping or fishing (Blench and Dendo, 2005). However, given the low number of H5N8 HPAI cases detected during autumn and winter 2017/2018 in the western Palearctic, it seems rather unlikely that new introductions into Western Africa occurred during the season of 2017/2018. The disease might be present in the region endemically in association with extensive duck production. So far no sequences of viruses from Nigeria have been published or submitted to public databases. This information is crucial for understanding the genesis and scope of the current outbreak and to determine whether any reassortment has occurred between co-circulating AI viruses.

Eastern Africa Two large-scale mortality events in white-winged black terns (*Chlidonias leucopterus*) on the coast of Lake Victoria, Uganda were the first occasion in which a novel H5 lineage Gs/GD/96 lineage H5N8 HPAI virus was detected in East Africa (Sims *et al.*, 2017; FAO, 2017). During January to February 2017 more cases and outbreaks followed involving domestic ducks and some unspecified domestic bird species, as well as unspecified wild species (OIE, 2017a) not only on the north-western coast of Lake Victoria, but also at nearby Lake Albert (Figure 3). In April the disease flared up in domestic poultry on the Democratic Republic of the Congo shore of Lake Albert and by June the situation evolved into a typical poultry epidemic with clusters of affected locations. It is not clear whether the cases in the Democratic Republic of the Congo in April were the first or whether other cases had not been detected (Twabela *et al.*, 2018; Wade *et al.*, 2018).

It is plausible that in East Africa the aquatic bird communities of at least two large wetland areas (Lake Victoria and Lake Albert) were

Figure 3
Distribution of H5N8 detections in East Africa in 2017



Source: WAHIS, OIE

subject to incursion of the novel H5N8 viruses, which also included the involvement of resident species and intra-African migrants. In November and early December 2017, the virus reappeared on the shores of Lake Albert in the Democratic Republic of the Congo, in the same area as the previous poultry epidemic, affecting domestic ducklings with 80–100 percent mortality in five coastal villages. An epidemiological link to the wild birds at the lake was suspected (OIE, 2018a). Unfortunately, because of lack of sequencing data, it is not possible to establish with confidence whether these outbreaks were due to a new seasonal introduction or disease persistence in the area. However, given the relatively rare occurrence of H5N8 HPAI in Europe at the time, a new introduction is considered less likely.

Arrival and circulation of a wide range of avian influenza viruses carried to Africa by Palearctic migrants and their further re-assortments and evolution in Afro-tropical ecosystems is in itself not unusual (Abolnik *et al.*, 2006). What seems to be unexpected in relation to the events of 2016/2017 is firstly the speed with which several closely related H5N8 viruses spread beyond the limit of the

Palearctic duck distribution in East Africa and secondly their subsequent rapid invasion into Southern Africa. The geographic expansion of the disease occurred during periods and along certain directions that strongly suggest considerable involvement of Afro-tropical aquatic birds (see also section on ecological drivers).

Southern Africa On 17 May 2017 H5N8 HPAI clade 2.3.4.4 was detected in a commercial broiler breeder operation in Harare, Zimbabwe with epidemiological evidence of a spillover from a nearby wetland (K. Manyetu, 2018 - personal communication). On 19 June the first outbreak in South Africa was detected in the town of Villiers likewise located near a waterway, the Vaal River. H5N8 HPAI also caused mortalities at a commercial breeder site 35 km away near Standerton, though no epidemiological links to previous outbreaks could be identified. Later, researchers from South Africa (Abolnik *et al.*, forthcoming), using full genome sequences and analysis of re-assortment patterns of H5N8 isolates, determined that introduction of H5N8 HPAI clade 2.3.4.4 to the north of South Africa

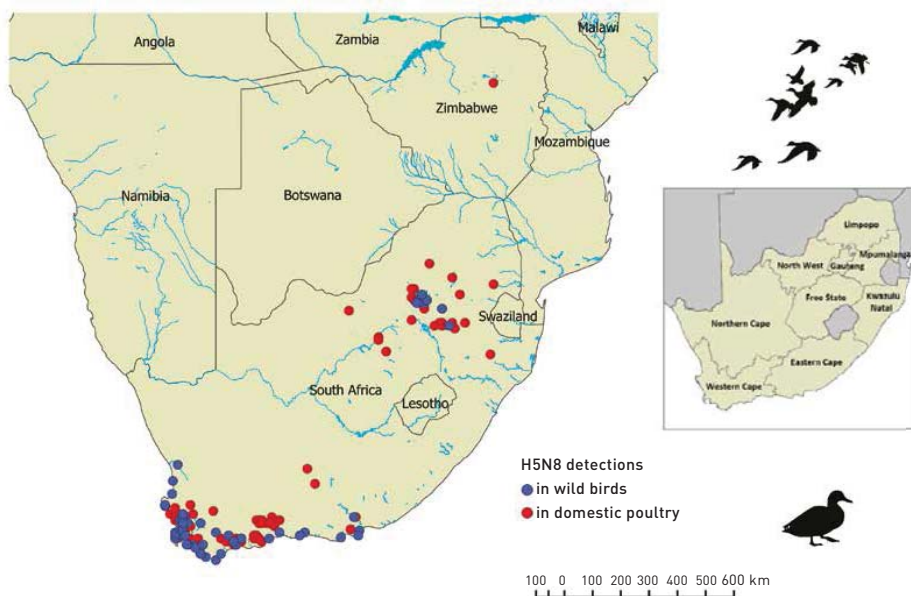
involved five virus variants within Group B of clade 2.3.4.4. This was apparently a multiple source incursion event, suggesting a wild-life origin for these poultry outbreaks. These findings strongly parallel earlier observations regarding outbreaks of the same H5N8 HPAI clade 2.3.4.4 in Egypt (Salaheldin *et al.*, 2018) and, in general, other similar multi-source events with historical invasions of H5 HPAI Gs/GD/96 lineage viruses elsewhere (Ducatez *et al.*, 2006; Marinova-Petkova *et al.*, 2014; Tosh *et al.*, 2016; Pohlmann *et al.*, 2017).

In South Africa the evolution of the H5N8 HPAI epidemic was documented in more detail compared to the rest of the continent due to more sensitive surveillance and prompt reporting. Since its first outbreak in June 2017, the country has notified the OIE of 192 H5N8 detections as of 18 July 2018. They formed two genetically distinguishable spatial clusters (Figure 4), the first in the northern provinces (n=36; Gauteng (14), Mpumalanga (12), North West (four), Free State (three), Limpopo (two) and KwaZulu-Natal (one) provinces). The second, much larger one was in the south (n=153; Western (144) and Eastern (9) Cape provinces). The virus was first discovered in sick poultry in the north and subsequently picked up by surveillance in the south: in the Western Cape the first detection was on an ostrich farm on 2 August 2017. This incursion developed into a massive epidemic (see details below) with a major peak in September 2017 and a second flare-up early in 2018, mainly due to the virus spreading to wild aquatic birds inhabiting coastal areas (Figures 4 and 5). Interestingly, preliminary molecular evidence suggests that the viruses from the northern and southern regions of South Africa, although genetically very similar, may have diverged before they reached the country. This means that the southern variant was probably introduced to the wild bird populations independently, maybe even around the same time as the one in the north, but was detected two months later.

In the north, mainly around the Pretoria – Johannesburg area, there were 20 outbreaks of H5N8 HPAI in poultry and nine cases in wild birds during June to October 2017. On one occasion the virus affected captive swans (*Cygnus spp.*). Ten reports of H5N8 HPAI in domestic or captive birds notified to OIE did not contain information on affected species. Of the remaining ten outbreaks, five were in

Figure 4

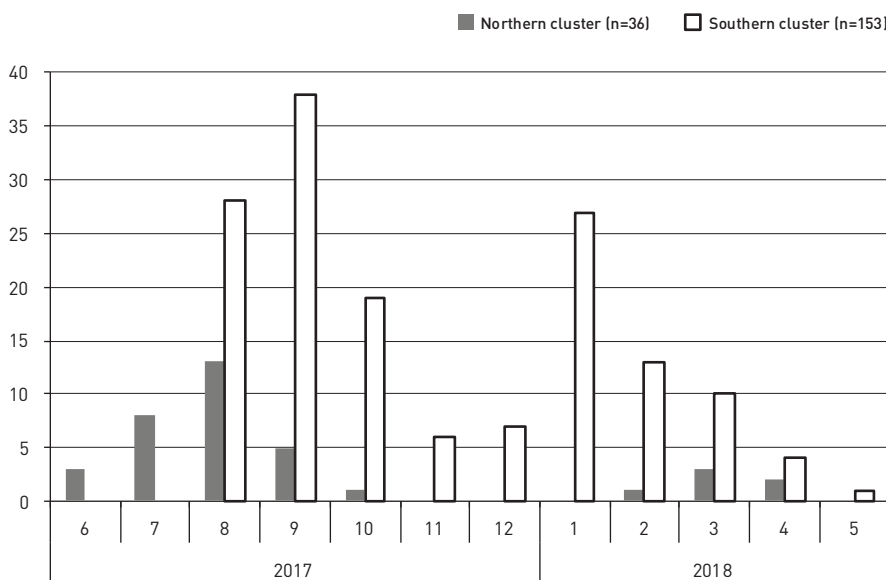
Two main geographical clusters of H5N8 HPAI notifications in South Africa (June 2017 – 31 May 2018)



Timeline of virus detections in all categories of avian hosts for the northern and southern clusters, separately. Inset map: Provinces of South Africa. Source: WAHIS, OIE

Figure 5

Monthly numbers of H5N8 notifications between June 2017 and 31 May 2018 in South Africa by clusters



Source: WAHIS, OIE

chickens, three in geese, one in ducks and one in a hobby swannery. Cases in (nominatively) wild birds included a) waterfowl: Egyptian goose - *Alopochen aegyptiaca* (two), Yellow-billed duck - *Anas undulata* (one); b) a scavenger: African sacred ibis - *Threskiornis aethiopicus* (two) and c) some farm associated species: African masked weaver - *Ploceus velatus* (two), house sparrow - *Passer domesticus* (one), blue crane - *Anthropoides paradisea* (one, captive), red-crowned crane - *Grus japonensis* (one, captive). Monthly frequencies of H5N8 HPAI detection in the two categories of species (domestic - including captive versus wild) were generally correlated, suggesting a parallel development of the epidemic in poultry and free-ranging wild species.

In the south, the first wave of the H5N8 HPAI epidemic in the country (August–December 2017, n=98) involved primarily domestic species (77 detections), with 20 detections of the virus in wild birds and one more in a holding with captive wild birds (Figure 6). The majority of poultry outbreaks with identified species included ostrich farms (39) followed by holdings with chickens (28), geese (nine), ducks (four),

and turkeys (two). Seventeen properties contained poultry kept for commercial purposes, including 15 commercial chicken farms and two duck farms. Twenty-one holdings contained birds kept for hobby or subsistence purposes and on seven holdings more than one species was affected. Ostriches appeared to be relatively resistant to this virus with few mortalities or clinical cases.

Confirmed cases in wild birds were reported also in 16 locations, sometimes several species at a time. Wild species killed by H5N8 HPAI during the first wave (August–December 2017) included: a) waterfowl: Egyptian goose - *Alopochen aegyptiaca* (one), spur-winged goose - *Plectropterus gambensis* (one); b) farm associated or synanthropic species: helmeted guinea fowl - *Numida meleagris* (three), blue crane - *Anthropoides paradisea* (two), laughing dove - *Spilopelia senegalensis* (two), pied crow - *Corvus albus* (two), speckled pigeon - *Columba guinea* (one), house sparrow - *Passer domesticus* (one); and c) raptors: peregrine falcon - *Falco peregrinus* (two) and a spotted eagle-owl - *Bubo africanus* (one). One report of helmeted guinea fowl - *Numida meleagris*

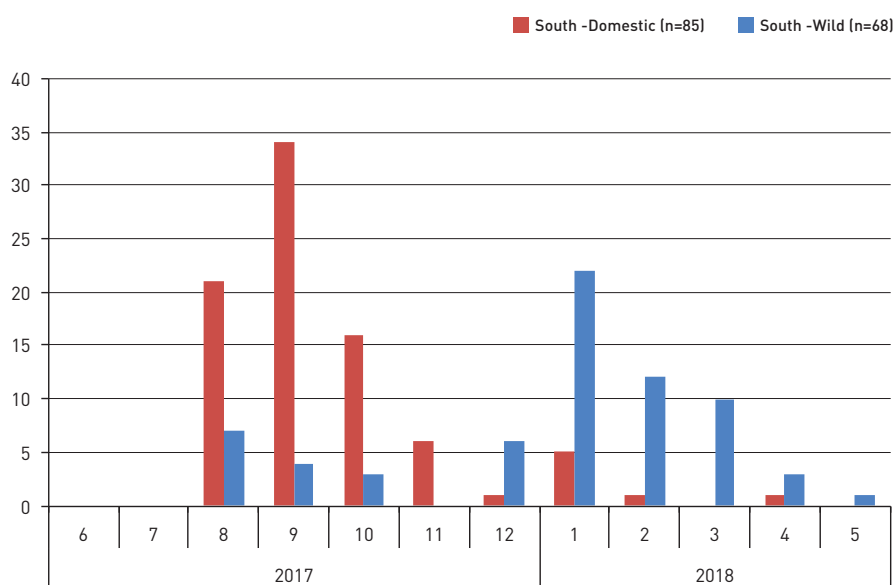
involved 40 birds found dead on one property and one report of blue crane - *Anthropoides paradisea* involved seven birds, three dead and four showing lethargy and diarrhoea, on a farm approximately 1.5 km away from an ostrich farm. The dead birds tested negative, but tracheal swabs from the live birds tested PCR positive. As these deaths in wild birds occurred at the height of the outbreaks in domestic birds, there were few resources available to test wild birds more extensively or further investigate reported deaths. Since the first detections in terns in December, the majority of deaths reported and positive cases have been in marine species (Figure 6 and Table 1).

Towards the end of 2017 detections of H5N8 in wild and domestic birds were declining (Figure 6) and reached their minima in November and December 2017, respectively. During these two months, there were only six ostrich holdings affected in the domestic sector. However, in December 2017 the virus was identified in coastal larids, an ecological group of wild birds in which the virus had not previously been detected during the 2017 winter season.

Dead and sick swift terns (*Thalasseus bergii*) tested positive at multiple locations in and around Cape Town, Hermanus and Port Elizabeth. The birds tested were mostly single birds found alive and alone on beaches and taken to rehabilitation facilities. There were reports from multiple locations of abnormal numbers of carcasses on beaches, the largest numbers at once being two or three reports of up to 20 birds, not close to any major breeding colonies, but at known tern roosts. The very first report of a relatively large number of dead seabirds was from the Bot River Estuary on 18 December and it involved 13 swift terns, seven Arctic terns (*Sterna paradisaea*) and one each of a kelp gull (*Larus dominicanus*), Hartlaub's gull (*Chroicocephalus hartlaubii*) and sandwich tern (*Thalasseus sandvicensis*). In the following months, the wildlife epidemic grew in scale (Figure 6). More affected terns of other species, as well as other birds, particularly those associated with coastal habitats, were found in January–May 2018 elsewhere in the Western and Eastern Cape Provinces (Figure 7 and Table 1). In March–April 2018 the virus killed thousands of juvenile birds at two breeding colonies of swift terns and over 340 at a third. More details on the wildlife species

Figure 6

Monthly numbers of H5N8 virus notifications between June 2017 and 31 May 2018 in the Western and Eastern Cape of South Africa by type (domestic*/wild)

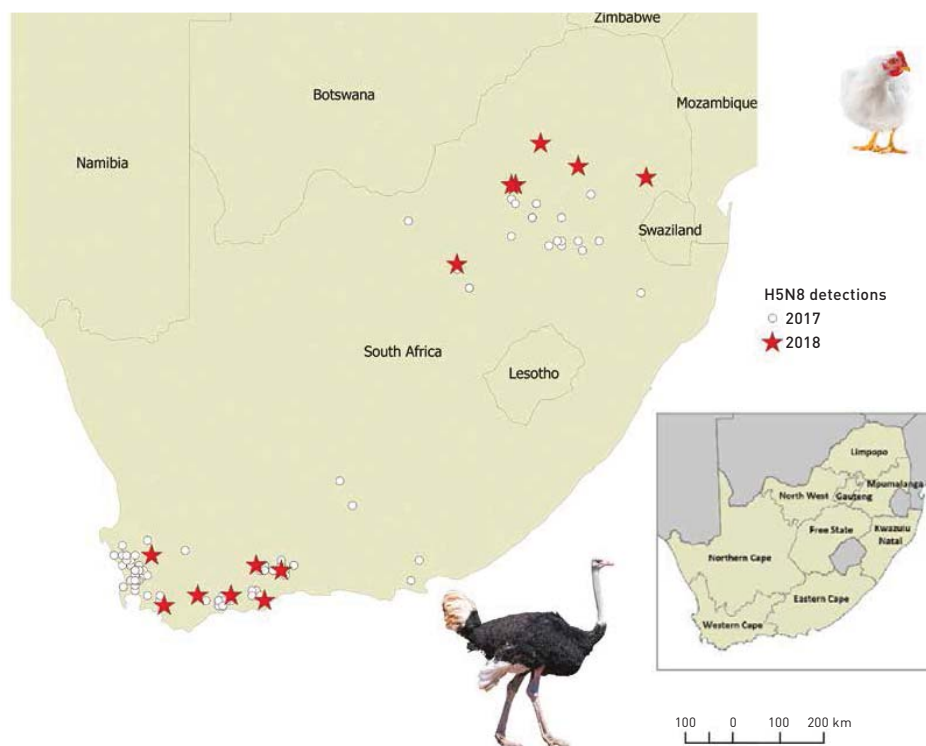


* domestic includes captive wild species.

Source: WAHIS, OIE

Figure 7

Outbreaks of H5N8 HPAI on poultry farms, zoos and hobby bird collections in South Africa during the period June 2017 to 31 May 2018



Inset map: Provinces of South Africa.

Source: WAHIS, OIE

affected and coastal epidemic of H5N8 in Western and Eastern Cape Provinces are provided on page 9 of the Focus below.

In February 2018 H5N8 HPAI re-emerged in the north of South Africa (Figures 5 and 7) and has so far affected six holdings (five poultry farms and one hobby swannery). As of June 2018, there is no evidence that the virus is persistently circulating in poultry, backyards or commercial farms. Veterinary authorities in South Africa are monitoring the situation intensively in both commercial and backyard sectors. Investigations are ongoing into whether the source of the virus was South Africa, or from variants that were circulating silently elsewhere. The backyard flocks that have recently tested positive seem to be low biosecurity mixed species flocks, with waterfowl that require a water body (pond or dam) on the property. This implies that the virus is likely to be present in wild bird reservoirs in the north of South Africa as well and could be introduced into poultry holdings at any time.

In spite of predominant detections of H5N8 virus in wildlife in 2018 and ongoing active AI surveillance in ostrich farms, in the south of South Africa, Western and Eastern Cape Provinces, the disease has only been occasionally diagnosed in ostriches (latest report 5 April 2018, Figures 6 and 7). During the current colder season, it was feared that avian influenza transmission and survival rates would increase in the whole of South Africa and lead to an upsurge of outbreaks in poultry in July/August, similarly to 2017. However, between 1 July and 15 August 2018 only one H5N8 notification was reported from South Africa to OIE, affecting a dead wild blue crane (*Grus paradisea*) in Western Cape Province. Nevertheless, the situation in poultry requires very close continuous monitoring not only in the country, but also in the whole of sub-tropical Africa, as the disease has a strong potential to develop rapidly into epidemics with heavy losses to the industry and smallholders. ●

Wild bird species affected by H5N8 HPAI in Africa and the South African epidemic in marine birds

There were just a few occasional detections of H5N8 in wild birds to the north of the equator, with mortality events in white-winged black terns (*Chlidonias leucopterus*) indicating that marsh terns (*Chlidonias spp.*) are highly susceptible to the virus. In North Africa, only three Palearctic species were found to test positive: Eurasian coot - *Fulica atra* (two) and Eurasian wigeon - *Anas penelope* (one) which were found dead as well as common teal - *Anas crecca*, which were asymptomatic (Kandeil *et al.*, 2017). There was also one isolate from a dead grey-headed gull - *Chroicocephalus cirrocephalus*, in Uganda (see phylogenetic analysis in Annex 1).

The white-winged black tern is a common wintering bird in East African wetlands. Specifically, Lutembe Bay, Uganda supports up to 70 percent of the global white-winged black tern population (up to 2.5 million individuals, on average >95 percent of all birds present), along with internationally important numbers of several other waterbirds (Byaruhanga and Nalwanga, 2006). Most likely, these abundant and highly gregarious terns overwintering at roosting sites served a role as sentinels to the presence of H5N8 infection in the ecosystem of Lake Victoria (FAO, 2017).

Passive surveillance in South Africa revealed a remarkably large range of species infected (n=25; Table 1), which can be arranged into four groups based on epidemiological considerations and knowledge of their ecology. Waterfowl seem to be clearly under-represented in the list (three species), which might indirectly suggest a mainly asymptomatic course of infection and could point to a reservoir role, as has been the case for other H5 HPAI Gs/GD/96 lineage viruses (Napp *et al.*, 2018). The raptor/scavenger group (five species) often become infected whenever a large AI outbreak in wild birds takes place (Van den Brand *et al.*, 2015). Those could have been exposed to the virus via the alimentary route by preying upon sick birds or scavenging on infected carcasses. Of the seven terrestrial species, some could have been associated with outbreaks in poultry,

Table 1

Species of free-living wild birds found to be infected in South Africa split into four eco-epidemiological groups with indication of the total number of H5N8 HPAIV detections in each species as reported to OIE

<GROUP/SPECIES>		<GROUP/SPECIES>		<GROUP/SPECIES>		
#	Marine & coastal (10, n=67)	#	Terrestrial (7, n=13)	#	Raptor/scavenger (5, n=9)	
1	<i>Thalasseus bergii</i>	34	11 <i>Numida meleagris</i>	3	18 <i>Bubo africanus</i>	2
2	<i>Spheniscus demersus</i> *	10	12 <i>Anthropoides paradisea</i> **	2	19 <i>Corvus albus</i>	2
3	<i>Sterna hirundo</i>	7	13 <i>Passer domesticus</i>	2	20 <i>Falco peregrinus</i>	2
4	<i>Phalacrocorax capensis</i> *	6	14 <i>Ploceus velatus</i>	2	21 <i>Threskiornis aethiopicus</i>	2
5	<i>Chroicocephalus hartlaubii</i>	4	15 <i>Spilopelia senegalensis</i>	2	22 <i>Buteo rufofuscus</i>	1
6	<i>Haematopus moquini</i>	2	16 <i>Columba guinea</i>	1		
7	<i>Thalasseus sandvicensis</i>	2	17 <i>Columba livia</i>	1	Waterfowl (3, n=6)	
8	<i>Chroicocephalus cirrocephalus</i>	1		23	23 <i>Alopochen aegyptiaca</i>	4
9	<i>Microcarbo coronatus</i>	1		24	24 <i>Anas undulata</i>	1
10	<i>Morus capensis</i> *	1		25	25 <i>Plectropterus gambensis</i>	1
Total (25 species, n=85)						

Please note that for many locations more than one species was reported, therefore the number of detections does not correspond to the total number of wild bird-related HPAI notifications to the OIE.
* EN: Endangered; ** VU: Vulnerable (International Union for Conservation of Nature - IUCN)

Source: WAHIS, OIE

particularly in open production systems such as for ostrich or domestic waterfowl, while others may have been exposed to other birds or aquatic reservoirs.

Marine birds made up the largest group of reported species mortalities and positive test results (see Table 1) which is indicative of their role in the circulation of H5N8 within the coastal ecosystem, particularly in and around Cape Town but also overall along the coastal zone for over 1 000 km (Olifants River Estuary to Port Elizabeth). Terns, particularly swift terns, comprised the worst affected systematic group (63 percent of detections – 43/68; greater crested tern - *Thalasseus bergii*, common tern - *Sterna hirundo*, sandwich tern - *Thalasseus sandvicensis*). The African penguin (*Spheniscus demersus*) was the second most reported species (15 percent – 10/68), followed by two species of cormorants (10 percent – 7/68; *Phalacrocorax capensis*, *Microcarbo coronatus*). Figure 8 illustrates locations of H5N8 events in South Africa involving these four species. There were also single detections in gulls (*Chroicocephalus cirrocephalus*, *Chroicocephalus hartlaubii*), waders (*Haematopus moquini*) and Cape gannet

(*Morus capensis*). These species comprise the coastal bird community and most are rarely seen inland. Close interactions between them at roosting and feeding sites commonly occur. Gulls also scavenge on carcasses of other birds opportunistically. At this stage, the true epidemiological role of different species of African wild birds based on these scattered but valuable observations is too speculative. Interpretation of the formal figures on the number of reported detections will be difficult as resources for testing dead birds were limited, priority was given to endangered species and sampling was also otherwise biased or opportunistic as is often the case with wildlife.

In addition to the list in Table 1 several local and exotic species in captivity (in or in association with zoos or bird parks) were found sick or dead in 2017 from infection with H5N8. They included sacred Ibis (*Threskiornis aethiopicus*), blue crane (*Anthropoides paradisea*), black-headed heron (*Ardea melanocephala*), mallard (*Anas platyrhynchos*), black swan (*Cygnus atratus*), domestic turkey (*Meleagris gallopavo*) and red-crowned crane (*Grus japonensis*). The species kept in captivity are not included in the table of “true wild species”. ●

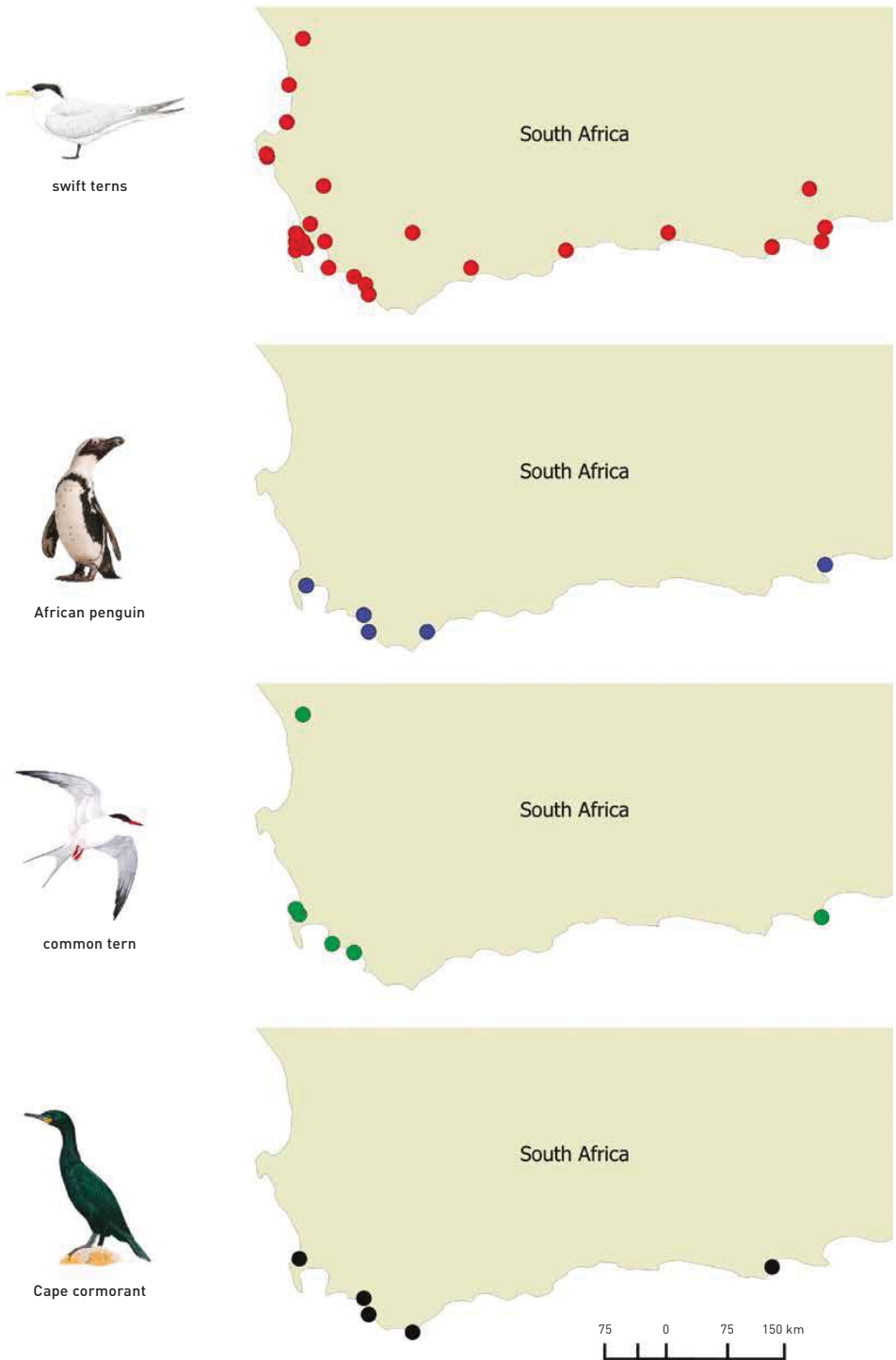
Environmental, epidemiological and phylogenetic observations and parallels

From Palearctic to Afro-tropical anatis Rapid spread of the novel H5N8 HPAI viruses from northern to southern parts of Africa within six months suggests they were apparently well adapted to infect and transmit to different avian species. This is further supported by their successful transcontinental expansion (Lee *et al.*, 2017; Napp *et al.*, 2018), as well as by experimental studies (Van den Brand *et al.*, 2018). H5N8 HPAI viruses were also likely circulating in the East African wetland ecosystems at an unusually high prevalence. The reasons for this might include the demographic composition of west Eurasian populations of overwintering dabbling ducks in 2016–2017 (Nallar *et al.*, 2015), as well as the cumulative effect of several environmental factors, which could be particularly favourable to southward expansion of H5N8 HPAI in Africa (see section below on the role of seasonal factors and anomalies).

Only a few species of non-tropical dabbling ducks reach epidemiologically significant

Figure 8

Geographical distribution of H5N8 detections in the four most frequently reported coastal species of wild birds in Western and Eastern Cape Provinces (June 2017 to 31 May 2018)



numbers to be able to spread and sustain circulation of avian influenza viruses in West Africa after their arrival at their wintering range. Of those, garganey - *Anas querquedula*, is the most abundant duck species, followed by northern pintail - *Anas acuta* and the northern shoveler - *Anas clypeata* (numerous only in the Senegal Delta). Among other Palearctic ducks, a few other species occasionally overwinter in sub-Saharan Africa: common teal - *Anas crecca*, eurasian wigeon - *Anas penelope*, common pochard - *Aythya ferina* and tufted duck - *Aythya fuligula* and, in rarer cases, common shelduck - *Tadorna tadorna* and some other ducks but they are usually in rather small numbers (Trolliet and Girard, 2006).

The wetlands in the Sahel zone in Africa are the principal wintering destination of ducks such as garganey, northern pintail and northern shoveler (Roux and Jarry, 1984; Trolliet and Girard, 2006). The most important overwintering sites are mainly located in its western part, the Senegal Delta, the Inner Niger Delta and Lake Chad Basin, although wintering congregations of garganey and northern pintail are also found in East Africa and as far south as the equator in Kenya and northern Tanzania (Trolliet and Girard, 2006; Scott and Rose, 1996). The apparent extensive redistribution of overwintering Palearctic anatids, both between years and within the same season, being dependent on hydrological conditions (Roux and Jarry, 1984), provides opportunities for virus maintenance and spread within sub-Saharan wintering areas (Figure 8). For these reasons, the incursion of the H5N8 HPAI virus, the first one of Palearctic origin, to Eastern Africa was expected, although unprecedented, except for a single isolated outbreak reported in southern Sudan in 2006 (OIE, 2006).

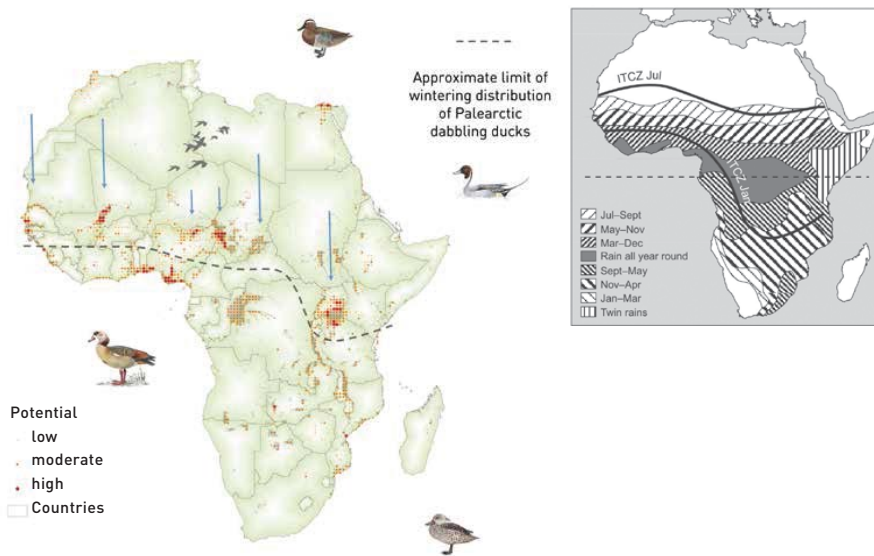
Role of seasonal factors and anomalies

Expansion of H5N8 HPAI to sub-equatorial Africa is very interesting from the standpoint of avian influenza ecology and can provide insights into the complex interplay of factors related to avian hosts' ecology, the role of environmental variables and virus properties. Historically, the distribution of Asian H5N8 HPAI viruses from the Gs/GD/96 lineage expanded in Eurasia during the winter months, shrinking back to the endemic countries or remaining in small, localized pockets of

Source: WAHIS, OIE

Figure 9

Semi-quantitative estimate of the introduction potential of HPAI H5 assuming involvement of wild aquatic birds in Africa



The estimate considers presence of all types of wetlands and extensive chicken density (Source: Dhingra *et al.*, 2016). The greyscale inset map shows generalized seasonal patterns of precipitation over the African continent (Source: Dodman and Diagona, 2007).

infection which would normally disappear in summer. This pattern was also generally followed by H5N8 HPAI, although local epidemics in some countries persisted for a somewhat longer time (e.g. Iran, Italy and Saudi Arabia; OIE, 2017b, 2018b, 2018c).

Provided a novel AI virus is introduced, there are several recognised factors that act synergistically to produce wintertime peaks in HPAI incidence and incursion risk in temperate regions in the Palearctic. They include: a) a generally higher degree of waterfowl aggregation at overwintering sites (Olsen *et al.*, 2006; Hill *et al.*, 2015); b) a higher proportion of immunologically naïve juvenile birds in the population in autumn and winter (Farnsworth *et al.*, 2012; Dijk *et al.*, 2014); c) cold spells that redistribute and further aggregate overwintering birds (Ottaviani *et al.*, 2010); and d) better environmental survival and transmission of AI viruses at low temperatures and humidity (Shaman and Kohn, 2009; Wood *et al.*, 2010; Farnsworth *et al.*, 2012). All of these factors working together in a certain year can dramatically increase the risk of virus spillover to domestic birds, potentially resulting in devastating epidemics in poultry. Such large-scale

poultry outbreaks may last well beyond the high incursion risk period due to various anthropogenic factors, husbandry, trade, effectiveness of disease control measures, etc. as long as there are sufficiently dense susceptible host populations.

In North and West Africa the 2014–2017 invasion of H5N1 HPAI, as well as the 2006–2009 incursion, had generally the same “Palearctic” seasonality. During the incursion phase, this could be naturally attributed to the arrival of overwintering anatids, but the introduced viruses continued to demonstrate the same January–March northern winter peak of incidence during the endemic phase, suggesting that seasonal environmental factors are involved in this dynamic.

Preliminary observations on outbreaks in Africa (Khomeenko *et al.*, forthcoming) suggest that low specific humidity (i.e. mass of water vapour in a unit mass of moist air, usually expressed as grams of vapour per kilogram of air) might be one factor involved in their occurrence. Additional data and analysis are needed to confirm the strength of this relationship and whether it can be used in forecasting.

If excluding involvement of human activities or movement, further southward expansion of the virus may have happened with increasing involvement of Afro-tropical aquatic birds. Given the very erratic movement patterns and complex seasonality of the life cycles of Afro-tropical water birds (Cumming *et al.*, 2016; Ndlovu *et al.*, 2017) it is difficult to implicate any particular group of species in the process, or to exclude the role of Palearctic migrants, such as charadriids. In any case, the first sub-equatorial detection of H5N8 HPAI in May 2017 in Zimbabwe correlates with cumulative monthly fledgling frequency of the most common Afro-tropical ducks in that area (Figure 10; Mundava *et al.*, 2016). The breeding schedules of white-faced whistling duck - *Dendrocygna viduata*, red-billed teal - *Anas erythrorhyncha*, knob-billed duck - *Sarkidiornis melanotos*, African pygmy goose - *Nettapus auritus*, and southern pochard - *Netta erythrophthalma*, demonstrate a seasonal pattern that produces an influx of juvenile ducks precisely in April to May, when spillover of H5N8 has the best chance of transmission among immunologically naïve individuals (Munster and Fouchier, 2009; Mundava *et al.*, 2016). Some of these duck species are known to undertake significantly long movements (Underhill *et al.*, 1999) so as to be able to spread the virus quickly in the sub-equatorial Africa. Ringing records demonstrate that these species undertake long distance local movements within southern Africa. Unfortunately, those records do not provide information on numbers of individuals involved or seasonal movement patterns of these species. However, a great part of such movement may result from waterbirds following rainfall patterns (Ferenczi *et al.*, 2016).

It is also worth noting that during the wet season (December 2016–April 2017, see Figure 10) a strong positive precipitation anomaly developed that was centred on Zimbabwe, Botswana and the northern part of South Africa, locally reaching up to 100 percent of the long-term normals. This possibly had a strong, positive effect on the numbers of breeding ducks, as well as on the outcome of their reproduction and thus may have been a conducive environment for the successful invasion of H5N8 into the Afro-tropical ecosystem that followed shortly afterward (Figures 4 and 5). Contrasting hydrological conditions along the wetland system of the Rift Valley with the

January drought in East Africa and abundant rainfall in Zimbabwe, Botswana and north of South Africa during the rainy season from December 2016 to April 2017 (Figure 10) might have stimulated a southern movement of Afro-tropical ducks with subsequent virus spread (Ferenczi *et al.*, 2016; Gaidet *et al.*, 2016; Harris *et al.*, 2013; Hurlbert and Liang, 2012).

As winter approached, the virus was also finding progressively drier and cooler conditions further southwards to facilitate its transmission and survival. In 2017 several related virus variants were subsequently discovered in South Africa (Abolnik *et al.*, forthcoming). Of these, variants that were isolated from outbreaks in the north of the country clustered with Egyptian and Eastern African H5N8 viruses from November 2016 to May 2017, while the variant introduced to the south of South Africa seems to be more related to the West African isolates (Nigeria and Cameroon). This adds plausibility to the hypothesis that the sub-equatorial expansion of H5N8 HPAI from November 2016 to May 2017 involved its increasingly broader circulation in sub-tropical African waterbirds, perhaps additionally facilitated by the effect of the preceding rainy season that was remarkably wetter than usual (see Figure 10).

The development of the H5N8 HPAI epidemic in South Africa generally mirrored earlier Gs/GD/96 lineage-like HPAI virus invasions in the Palearctic, but demonstrated a “reversed” seasonal peak. The virus detections increased during the southern winter and reached their respective maxima in August–October at a time when specific humidity dropped to its seasonal lows - conditions generally most favourable for better survival and transmission of influenza viruses. In sub-equatorial Africa, this period is epidemiologically equivalent to the elevated AI activity period in the Palearctic. For example, previously in the Western Cape, the incidence of the South African endemic AI viruses in ostriches increased during the southern winter (July/August) and dropped to a minimum in March/April (Abolnik *et al.*, 2016).

Contrary to the declining incidence of H5N8 HPAI in South African poultry populations, the southern summer brought an unexpected flare-up of disease in wild coastal birds. This mostly affected swift terns and expanded to their breeding colonies (see the

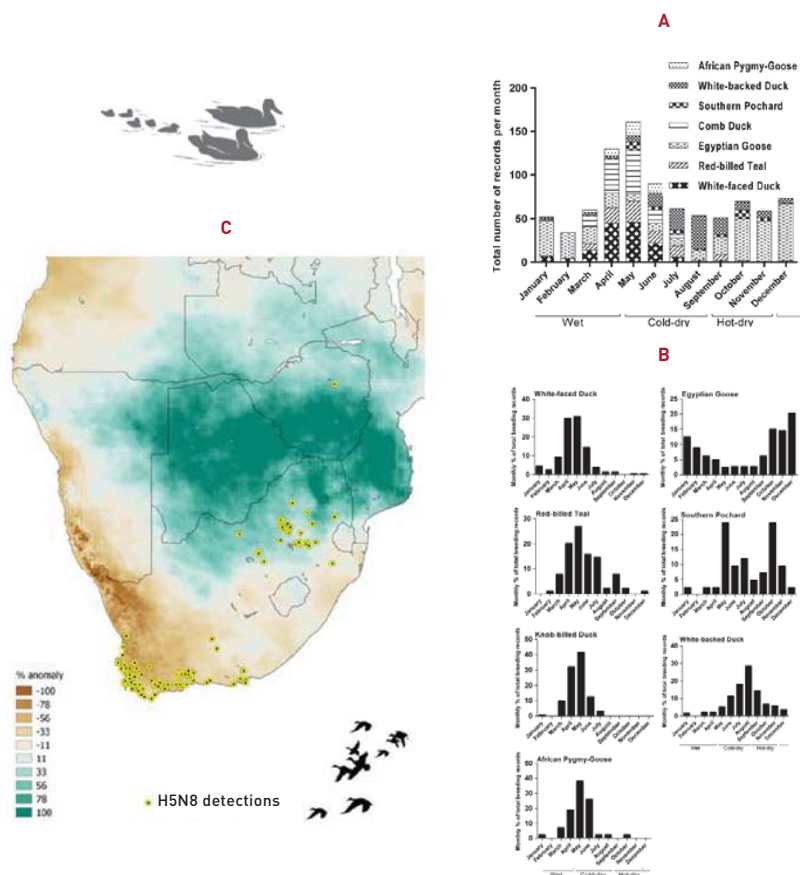
section on wildlife for more details). Such mass mortality events in breeding aquatic birds most closely resemble a series of recurrent H5N1 outbreaks in 2005 to 2015 at a number of endohoreic saline lakes in Central Asia (Qinghai Lake in China, several lakes in Mongolia, Lake Ubsu-Nur in Mongolia/Russian Federation and some others), during which several local breeding species were fatally affected, sometimes in remarkably large numbers (Sharshov *et al.*, 2012; Savchenko *et al.*, 2012; IFAO, 2016). Similar “residual” outbreaks of H5N1 HPAI, involving breeding cormorants (Ukraine in 2006; Chirniy *et al.*, 2008) or pelicans (Romania and Bulgaria in 2015; Stoimenov *et al.*, 2018) have occurred

in Europe, though much smaller in scale and duration. With regards to H5N8, however, substantial mass mortalities have been described in the Netherlands during the northern hemisphere autumn and winter of 2016 to 2017, especially among tufted ducks – *Aythya fuligula* (Kleyheeg *et al.*, 2017). These sporadic events, tailing more extensive winter-time epidemics, were typically associated with cold spells and died out soon after the arrival of warm summer weather.

A remarkable exception to the normal seasonal pattern of historical HPAI dynamics in the Palearctic was the summer 2006 H5N1 HPAI epidemic which occurred in the south of Western Siberia, Russian Federation

Figure 10

Considerations regarding the potential involvement of Afro-tropical water birds in H5N8 virus spread in Southern Africa



A. Cumulative seasonality of Zimbabwean duck fledgling as a proxy for numbers of juveniles in the population and monthly duck flock immunity rates (Source: Mundava *et al.*, 2016); B. seasonal fledgling patterns of the seven commonest Afro-tropical ducks (Mundava *et al.*, 2016); C. total precipitation rates percentage difference from 1981 to 2018 baseline mean for the period from 1 December 2016 to 30 April 2018 as a proxy for breeding conditions of waterfowl (Source: Climate Engine, 2018).

Figure 11

Total reservoir water stored in the Western Cape's largest six dams from 30 June 2013 to 15 January 2018



The graph illustrates the declining water storage levels during the Cape Town water crisis.

Source: Climate Systems Analysis Group (CSAG).

(Sharshov *et al.*, 2012). This unusual disease event involving both wild and domestic species took place in the middle of the northern summer (July–August).³ This, to some extent, resembled the epidemiological situation in the Western Cape over December 2017–March 2018, where the H5N8 epidemic in wildlife also escalated during the southern summer. Of note are the epicentres of wildlife mortalities in the Western Cape and Cape Town regions, affected by the worst drought in decades, starting from 2015 and by early 2018 leading to a massive and unprecedented decline of surface water reserves (Figure 11). A climatic anomaly of such magnitude is likely to have had a severe impact on the distribution of marine and freshwater aquatic birds, altering the normal patterns of their habitat use and interactions and potentially influencing H5N8 transmission dynamics and spread. During the northern winter, the Southern African ecosystems host a large number of overwintering Palearctic charadriids (Ryan, 2017), whose occasional involvement in the AI transmission chain in this part of the world

can apparently extend for months (December 2017–May 2018), facilitating persistent circulation of virus through the southern summer and autumn, which are generally less favourable for epidemic spread of AI in poultry.

In a broader historical perspective, the H5N8 outbreak in swift terns bears a striking resemblance to the mass mortality event in common terns *Sterna hirundo* in April–May 1961 in exactly the same area (Rowan, 1962; Becker, 1966). Ongoing investigation into the possible role of climatic and ecological factors should bring more understanding of the place of such rare puzzling events within avian influenza host–pathogen–environment dynamics. Notably, both events occurred two years after strong El Niño episodes that were followed by decreased precipitation and meteorological drought (Koopman and Buys, 2017; Barnard *et al.*, 2017).

Phylogenetic account Analyses of the phylogenetic topologies reveal that the HA gene sequences obtained from the African continent are dispersed throughout the tree of H5N8 virus clade 2.3.4.4.b sequences (see Figure 12 and Annex 1), indicating the occurrence of several independent introductions of the H5N8 HPAI virus into African domestic and wild bird populations. The genetic variability observed, along with the similarity to viruses circulating in Europe, the Middle East and Central and South Asia, confirms that wild birds did play a major role in the multiple introductions of the virus into the

continent. In particular, an in-depth analysis of the clustering of the HA genes obtained from sub-Saharan Africa indicates the occurrence of at least two distinct viral introductions into Cameroon. The HA genes of the viruses from Uganda and the Democratic Republic of the Congo cluster together with the virus A/duck/Cameroon/17RS1661-3/2017 identified in a Yagoua poultry market in the northern part of Cameroon (similarity 99.5 percent; Wade *et al.*, 2018). Interestingly, a lower HA gene similarity (group mean identity of 98.9 percent) was identified between the viruses from Central and East Africa and the strains detected in South Africa and Zimbabwe. Indeed, the sequences of the viruses collected from these Southern regions grouped together and with H5N8 HPAI viruses collected in domestic and wild birds in West Africa, Europe, Central and South Asia (group mean identity of 99.3 percent).

As already mentioned, preliminary molecular clock evidence from South Africa suggests that the viruses from the northern and southern regions, although genetically very similar, might have diverged before they reached the country. This means that the southern variant was probably introduced to the wild bird populations independently and around the same time as the one in the north, but was detected only two months later. Sequence data from 2018 in South Africa, so far unpublished, further indicate that the virus from the backyard outbreak, affecting domestic ducks and quail in North-West Province in April 2018, and the first winter spillover to commercial poultry in mid-June 2018, affecting pullets in Southern Gauteng, are genetically closely related to each other but different from viruses that circulated in these regions in 2017. The nucleoprotein gene of this new variant appears to be the most divergent and is clustering with the viruses isolated in Uganda, the Democratic Republic of the Congo and Cameroon. Either the new variant was present in 2017 but remained undetected, or it was introduced only recently, i.e. in 2018.

These data indicate that West Africa may have been the epicentre for the H5N8 spread in sub-Saharan Africa. However, the limited availability of genetic data prevents exclusion of the possibility that viruses more similar to the ones identified in central, eastern and southern parts of Africa were circulating in unsampled locations. Intensification of

³ The reader should note that, at the time of publication, the Russian Federation had reported 54 H5N8 HPAI outbreaks in poultry in: Kurskaya (six), Nizhegorodskaya (two), Orlovskaya (six), Penzenskaya (nine), Rostovskaya (three), Samarskaya (thirteen), Saratovskaya (three), Smolenskaya (two) Oblasts and Chuavashiya (seven) and Tatarstan (three) Respublikas from 7 June to 15 July 2018 (OIE), an event that still needs to be investigated and analysed for significance.

and the Democratic Republic of the Congo, cannot be excluded either. While wild bird migration from South Africa to the breeding areas in the Palearctic is usually direct with few stopovers, as compared to the risk of spread during the migration from breeding to the wintering areas in milder climates, there are a number of migratory bird species that could act as vectors moving northwards towards their breeding grounds into Africa, Europe and Asia.

Surveillance for AIV in both wild birds and poultry in most of Africa remains scattered, opportunistic and insufficient to respond to challenges such as repeat virus incursions. Patterns of disease spread, complicated particularly by the co-circulation of two HPAI viruses (H5N1 and H5N8), cannot be unravelled without the help of genomic epidemiology, which requires investment in field investigations, sample collection, sample dispatch with adequate preservation and sequencing of isolates for their analyses. In addition, the complexity of AI epidemiology involving multiple poultry and wildlife host species requires better definitions and use of standardized protocols for the collection of outbreak information. Outbreak investigations in wildlife are particularly challenging and resource-demanding activities, which should be managed and funded as part of each country's AI response plan or, alternatively, as a regional approach (i.e., commitment through a Southern African Development Community - SADC directive). Quality, standardized epidemiological data need to be collected, combined with strategic collection of viral sequences that are linked to epidemiological data and shared in a timely fashion both nationally and internationally. In southern Africa, lack of sufficient funding mechanisms to provide compensation to owners of infected animals culled as part of national control measures likely contributes to the reluctance of poultry owners to report disease and decreased sample submission to national veterinary laboratories, especially if the virus causes little clinical disease in ostriches. Proper policies in compensation schemes, if planned well, can trigger early reporting and thus prevent further disease spread, an issue of concern not only throughout the African continent but globally. As such this should receive adequate attention from the authorities as part of AI contingency planning.

Circulation of H5N8 virus among coastal birds in South Africa is the first documented

HPAI event to date of such magnitude in wild birds in Africa. Disease detections spanned coastal areas over more than 1 000 km and as of now continued for over 6 months. Such an extended H5N8 epidemic beyond the normal seasonal influenza activity period affecting this large number and variety of wild bird species has not been reported before for any other HPAI virus. Managing the disease in wild birds, particularly in mainland African penguin colonies, continues to be a challenge for conservation authorities. Little can be done to reduce the spread of the virus in the wild, other than swift carcass disposal whenever possible, and even this poses massive logistical challenges since it has proven difficult to identify a disposal method that is both feasible and effective. Efforts were made to raise public awareness about the presence of the virus in penguin colonies without creating undue anxiety, so as to limit the spread via humans to domestic poultry. Discussions were held on the need to close these colonies to the public, but eventually it was concluded that the risk of spread via wild birds was far greater than via human activity. The negative effects of closing the colonies to visitors could also outweigh any advantages as the maintenance of the reserves relies on income from visitors. However, monitoring and research programmes at the penguin colonies were temporarily halted with the aim to reduce stress for the African penguin and prevent possible spread of the virus through equipment used by management and research staff. Acknowledging this measure had a negative impact on long term monitoring and research, it was deemed a necessary precaution.

It is of great concern that this virus has reached and affected endangered marine bird species. It is challenging to make management decisions since there is no experience of handling similar outbreaks. Resources that would enable a more thorough investigation of the disease and its epidemiology in these species are also lacking. It has always proven difficult to determine the behaviour of an infectious agent in wildlife systems, since other unknown factors or variables may contribute to infection dynamics to a greater or lesser degree. Nevertheless, with the resources to hand, South Africa is making considerable effort to understand the disease and surveillance as well as outbreak management are

being carefully planned. The situation in South Africa requires further monitoring and investigation as such wildlife epidemics could occur elsewhere, particularly during dry seasons and anomalous droughts in other parts of Africa.

With increased understanding of the geographical scope and nature of the processes affecting AI host-pathogen-environment systems and the potential for trans-continental spread of AI viruses through wild birds, the research community and governmental sector should aim to establish closer and more practical inter-disciplinary collaboration in the spirit of "One Health", in order to be better prepared and respond more effectively to disease introduction and spread. ●

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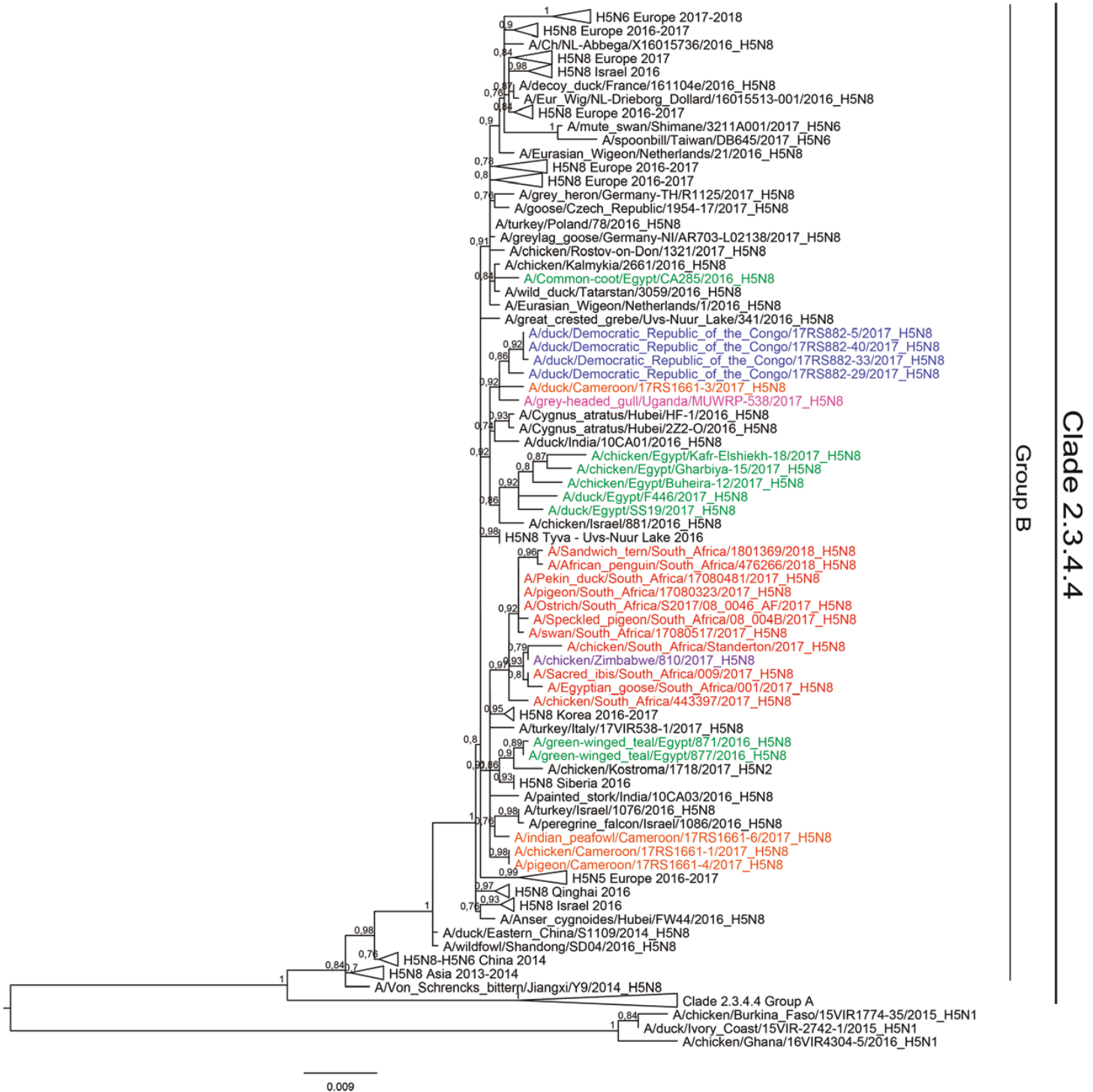
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ANNEX 1. Phylogenetic analysis of H5N8 virus sequences isolated globally



Some sequences in the phylogenetic analysis were from the Global Initiative on Sharing All Influenza Data (GISAID); the authors gratefully acknowledge the originating and submitting laboratories who contributed sequences to GISAID (www.gisaid.org). Please see here for full list . The authors are also most grateful to the Department of Livestock and Veterinary Services, Zimbabwe, for their permission to include the isolate A/chicken/Zimbabwe/810/2017_H5N8 in the phylogenetic analysis.

Sequence acknowledgment table available at http://www.fao.org/ag/againfo/programmes/en/empres/documents/docs/sequence_acknowledge_table_FA0.xls



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