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Antibody prevalence to avian influenza virus subtypes H5, H7 and H9 in falcons, captive and wild birds, United Arab Emirates, 2003–2006

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Abstract

Background: Avian influenza viruses (AIV) may cause enormous economic losses in the poultry industry and sporadically severe disease in humans. Falconry is a tradition of great importance in the Arabian Peninsula. Falcons may catch AIV through contact with infected quarry species.

Objectives: Falcons together with other bird species are the focus of this seroprevalence study, carried out on sera collected in the United Arab Emirates (UAE). AIV with the haemagglutinin subtypes H5, H7 and possibly H9 may infect humans.

Methods: We investigated the antibody prevalence to these subtypes in falcons and other birds by haemagglutination inhibition test. 617 sera of falcons and 429 sera of 46 wild/captive bird species were tested.

Results: From the falcons, only one was positive for H5 antibodies (0.2%), none contained antibodies to H7, but 78 had antibodies to H9 (13.2%). Regarding other birds, eight were positive for antibodies to H5 (2.1%), none had antibodies to H7, but 55 sera from 17 species contained antibodies to H9 (14.4%).

Conclusions: In contrast to H5 and H7 infections, H9N2 is widespread worldwide. Its ability to reassort, thereby creating possibly pathogenic strains for humans, should remind us of the potential risk that close contact with birds entails.

KEYWORDS
antibody prevalence, avian influenza, falconry, United Arab Emirates, wild birds

1 | INTRODUCTION

Avian influenza viruses (AIV), genetically distinct subtypes of influenza A viruses (IAV) usually found in birds, may cause in its highly pathogenic form a catastrophic disease, mainly in various species of domesticated birds, characterised by high morbidity and mortality, thus leading to enormous economic losses. Spillover infections may occur in humans following close direct contact with infected birds (Liu et al., 2017; Neumann & Kawaoka, 2015; World Health Organization [WHO], 2018). Wild aquatic birds, which constitute the natural reservoir for AIV (Olsen et al., 2006; Webster et al., 1992), can widely propagate viruses along their migration routes (Peterson et al., 2007; Reed et al., 2003; Tian et al., 2015; Xiao et al., 2007) by transmitting them to resident populations and domestic poultry (Hill et al., 2012; Verhagen et al., 2014). The recent introduction and spread of H5N1 AIV in wild bird species in North America demonstrates the topicality of AIV including zoonotic and public health aspects (Stokstad, 2022). Falcons, and the traditional hunting with these animals, have been of great importance in the Arabian Peninsula for centuries. Before the wealth of oil and gas changed the lives of many Arabs so dramatically, they had lived as Bedouins in and from the desert. At that time, falconry was not a sport, but a necessity to survive in this arid region. Today, in the United Arab Emirates (UAE) and its neighbouring countries, there is still a considerable demand for falcons to maintain this ancient Arab tradition, although nowadays more falcons are flown in falcon races rather than used for hunting wild birds. However, many hunters travel with their falcons to Pakistan and other Asian countries to hunt houbara bustards (*Chlamydotis undulata*) (Naguib et al., 2015). The potential contact with infected quarry, the consumption of this meat and the close contact with other wild/captive birds in aviaries make falcons potential carriers of AIV. Thus, they are at the centre of interest of this retrospective AIV seroprevalence study of birds in the UAE, together with a wide variety of other local, captive and wild bird species.

AIV are pathogens with zoonotic potential that primarily affect birds, but also a wide range of mammals (Webster et al., 1992). The different subtypes are classified according to their surface proteins haemagglutinin (H or HA) and neuraminidase (N or NA) (WHO, 2018). After the discovery of two new subtypes in bats in Central and South America, IAV are currently divided into 18 HA and 11 NA subtypes, of which 16 HA and 9 NA subtypes belong to AIV (Tong et al., 2012; Tong et al., 2013). IAV can further be classified according to the original host animal, for instance as avian influenza subtypes H5N1 ('bird flu') or H9N2, or as swine influenza subtype H1N1 ('swine flu') (WHO, 2018). Most AIV cause only mild infections in poultry and therefore belong to the group of low pathogenic avian influenza (LPAI) viruses, whereas those leading to severe disease and high mortality are designated highly pathogenic avian influenza (HPAI) viruses (WHO, 2018). H5 and H7 LPAIV may acquire increased virulence by mutations, thereby becoming HPAI viruses (Jonges et al., 2014).

All influenza A viruses have a segmented genome comprised of eight RNA segments, which code for the different RNA polymerase subunits, glycoproteins (HA, enabling viral entry, and NA, enabling viral release), nucleoprotein, matrix protein, membrane protein, nonstructural protein and nuclear export protein (Krammer et al., 2018). When a single host is infected by two different influenza A viruses at the same time, gene segments may be exchanged, which can result in a novel virus by reassortment (Short et al., 2015; Yoon et al., 2014). Influenza infection requires the presence of appropriate receptors on host cells for the viral HA to bind (Nelli et al., 2010). Previous studies had shown that AIV preferentially bind to sialic acid α2,3-galactose- (SAα2,3-Gal) linked receptors, while human influenza viruses exclusively bind to sialic acid α2,6-galactose- (SAα2,6-Gal) linked receptors (Rogers & Paulson, 1983). Because pigs express both on the epithelium of their respiratory tract (Nelli et al., 2010), they have been considered for a long time as potential 'mixing vessels' for avian and human influenza viruses to reassort (Scholtissek, 1990). However, more recent studies revealed that pigs express avian-like receptors only at minimum levels, while they are more abundant in humans than previously thought (Nicholls et al., 2007; Trebbien et al., 2011; van Poucke et al., 2010). Moreover, the expression patterns in pigs and humans are highly similar, suggesting that pigs are not more suitable as 'mixing vessels' than humans (Nelli et al., 2010). These reports fit well to the observation that the vast majority of human infections with zoonotic influenza viruses have emerged due to direct human contact with infected birds (Fouchier et al., 2004; Gray et al., 2007; Li et al., 2014; Tahir et al., 2019). Therefore, also the close contact to birds in falconry may increase the risk of interspecies transmission, especially during training with live quarry derived from animal markets and when hunting waterfowl.

Although human infections with zoonotic IAV are rare, any emerging strain with the ability to transmit from human to human may cause a pandemic (Jonges et al., 2014; WHO, 2018). Patients infected with an H5 or H7N9 AIV often develop high fever, cough and difficulty in breathing, complications may lead to respiratory failure, septic shock and multiorgan dysfunction. Therefore, the case fatality rate of these infections is much higher compared to seasonal influenza (Li et al., 2014; WHO, 2018). Infections with H7N7 or H9N2 usually cause only mild symptoms in humans, and so far only one fatal H7N7 infection has been reported (Fouchier et al., 2004; WHO, 2018). In general, H5, H7, and possibly H9 (in this order), are the most dangerous AIV HA subtypes for humans. Thus, we investigated the antibody prevalence to these subtypes in falcons and other captive/wild birds by haemagglutination inhibition (HI) test, a standard serological assay for detecting and measuring AIV subtype-specific antibodies, recommended by the World Organisation for Animal Health (WOAH) for the detection of avian influenza virus HA immune responses in their

Impacts

- Predominantly antibodies to the H9 avian influenza virus subtype were found in birds used for falconry in the UAE 2003–2006.
- No antibodies to H7, and only marginal levels of H5 antibodies were detected.
- The ability of the H9N2 subtype to reassort might pose a risk to public health.

latest edition of the OIE Terrestrial Manual (2021: https://www.woah.org/fileadmin/Home/eng/Health_standards/tahm/3.03.04_AI.pdf, page 3, B. Diagnostic techniques; Table 1) (World Organisation for Animal Health [WOAH], 2021).

2 | MATERIALS AND METHODS

In total, 617 serum samples from falcons and 429 sera from 46 different wild/captive bird species have been tested for H5N1, H7N1 and H9N2 antibodies. All samples were collected from 2003 through 2006. The majority were obtained from the blood bank of Dubai Falcon Hospital (DFH), and the remaining samples were collected in Dubai from October through December 2006. The origin of the falcons was known in most cases, even though it cannot be excluded that some falcons declared as captive-bred were actually wild caught. From the other bird species, some were born in private zoos in the UAE, some were imported from breeders in the Middle East or Europe, and some, such as the mallards sampled from a private lake in Dubai, and potentially wild caught houbara bustards which were suspected to have been imported from Pakistan, were obviously of wild origin. Unfortunately, in the files of the blood bank no data were available about the clinical status of the birds before or at the time of sampling; however, their vaccination status was clearly documented. The blood samples collected by the author were all from clinically healthy birds. Samples from birds which had been vaccinated were excluded from the study.

2.1 | Blood sample collection

Blood samples were collected from the basilic vein (*Vena cutanea ulnaris superficialis*), the right jugular vein (*Vena jugularis dextra*) or the caudal tibial vein (*Vena metatarsalis plantaris superficialis*). Venipuncture was performed using a 23-gauge needle and a 1-mL syringe. The bird sera were stored at −28°C until serum collection was completed. The HI test procedure was done according to the WOAH manual of diagnostic tests and vaccines for terrestrial animals (WOAH, 2021). After completing the tests, samples from the same individuals with the same results were removed from the original sample list. Subsequently, 592 samples from five falcon species plus falcon hybrids, and 383 serum samples of 46 other bird species remained for further investigation, resulting in a total of 975 samples tested.

2.2 | Haemagglutination inhibition (HI) test

In this study, the seroprevalence of antibodies to H5N1, H7N1 and H9N2 AIV subtypes was investigated by HI test, as the HI test is a well-established standard assay for the detection of subtype-specific AIV antibodies, and it has been shown that HI and virus neutralisation antibody titres correlate quite well (Pitisuttithum et al., 2017; Segovia et al., 2019). After heat inactivation of the sera at 56°C for 30 min, adsorption with freshly collected chicken red blood cells (RBCs) was performed to avoid non-specific agglutination. The serum was then diluted twofold with phosphate-buffered saline and mixed with four haemagglutinin units of inactivated H5N1, H7N1 and H9N2 viruses, respectively. After 30 min incubation at room temperature (RT), 1% washed, specific pathogen-free chicken RBCs were added to the wells and the mixture was again incubated at RT for 30 min. The procedure was carried out in U-shaped 96-well microtitre plates. The HI titre was defined as the highest serum dilution that causes a complete inhibition of erythrocyte agglutination. A titre of 1:16 or higher was considered positive, as recommended by WOAH (WOAH, 2021).

2.3 | Viruses used

The following virus strains were used in the HI assays: the β-propiolactone-inactivated H5N1 AIV wild-type strain A/Vietnam/1203/2004, the 0.1% formalin-inactivated H7N1 D 2368/03 strain and the H9N2 strain A/Quail/Dubai/302/2000.

3 | RESULTS

Table 1 and Figure 1 give an overview of the results of all investigated sera. In total, 56 wild/captive birds (14.6%; corrected for seven double-positive birds) and 79 falcons (13.3%) tested positive for antibodies

TABLE 1 Overview of the results of all falcons and other wild/captive birds investigated by HI test for antibodies to H5N1, H7N1 and H9N2 AIV subtypes.

			Reciprocal HI titre[a] [*n*]									
Sample pool	***n***	**H5/H7/H9**	**neg.**	**16**	**32**	**64**	**128**	**256**	**512**	**1024**	**Pos. [*n*]**	**Pos. [%]**
Wild/captive birds	383	H5	375	3	3		1		1		8	**2.1**
		H7	383								0	**0.0**
		H9	328	14	16	4	10	3	4	4	55	**14.4**
Total	383	H5/H7/H9	327	17	19	4	11	3	5	4	56	**14.6**
Falcons	592	H5	591		1						1	**0.2**
		H7	592								0	**0.0**
		H9	514	35	29	9	4	1			78	**13.2**
Total	592	H5/H7/H9	513	35	30	9	4	1	0	0	79	**13.3**

Total numbers of wild/captive birds were corrected for individual double-positive birds ($n = 7$).
[a]Titres ≥1:16 were considered positive.

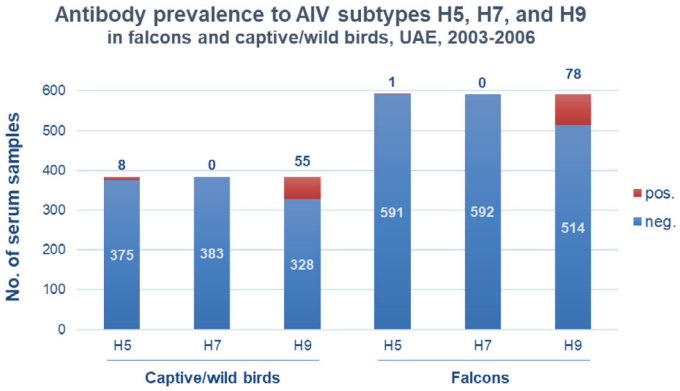

FIGURE 1 Antibody prevalence to AIV subtypes H5, H7 and H9 in falcons and wild/captive birds, UAE, 2003–2006. The vertical axis indicates the number of samples investigated. Columns 1–3 depict the prevalence of antibodies in sera of wild and captive birds, columns 4–6 the prevalence in falcon samples. Columns 1 and 4 represent the results for antibodies to H5, columns 2 and 5 the results for H7, and columns 3 and 6 for H9. The negative portion of samples is shown in blue, and positive samples are given in red.

TABLE 2 Detailed list of all falcons investigated by HI test for antibodies to H5N1, H7N1 and H9N2 AIV subtypes.

			Reciprocal HI titre[a] [*n*]								
Order/species	***n***	**H5/H7/H9**	**neg.**	**16**	**32**	**64**	**128**	**256**	**512**	**1024**	**Pos. [%]**
Falconiformes											
Lanner falcon (*Falco biarmicus*)	3	H5/H7/H9	3								
Saker falcon (*Falco cherrug*)	74	H5/H7	74								
		H9	67		4	2	1				**9.5**
Barbary falcon (*Falco peregrinus pelegrinoides*)	5	H5/H7/H9	5								
Peregrine falcon (*Falco peregrinus*)	117	H5/H7	117								
		H9	113	1	1		1	1			**3.4**
Gyrfalcon (*Falco rusticolus*)	86	H5/H7	86								
		H9	75	5	5	1					**12.8**
Gyrfalcon hybrid (*Gyrfalcon x sp.*)	307	H5	306		1						**0.3**
		H7	307								
		H9	251	29	19	6	2				**18.2**

[a]Titres ≥1:16 were considered positive.

to any of the three AIV subtypes (Table 1). A detailed list of species-specific results for all falcon and other bird samples is shown in Tables 2 and 3, respectively.

From 592 falcon samples investigated, only one gyrfalcon hybrid was positive for H5 subtype antibodies (0.2%), none contained antibodies to H7 (0.0%), but 78 had antibodies to H9 (13.2%). More specifically, 4 out of 117 peregrine falcons (*Falco peregrinus*; 3.4%), 11 out of 86 gyrfalcons (*Falco rusticolus*; 12.8%), and 7 out of 74 saker falcons (*Falco cherrug*; 9.5%) were positive for H9 antibodies (Table 2). Regarding the gyrfalcon hybrids, only 1 out of 307 samples contained antibodies to H5 (0.3%), but 56 sera were positive for H9 (18.2%).

Similar to the falcon samples, out of 383 other wild/captive birds tested, 55 sera from 17 different species contained antibodies to H9 (14.4%). As shown in Table 3, eight birds were positive for antibodies to H5 (2.1%), namely two wild turkeys (*Meleagris gallopavo*), one maned duck (*Chenonetta jubata*), one ringed teal (*Callonetta leucophrys*), one greater flamingo (*Phoenicopterus roseus*) and three lesser flamingos (*Phoeniconaias minor*). No antibodies to H7 were detected in any sample above threshold. Because only small numbers of samples were tested for most species, it is difficult to draw general conclusions. However, in wild turkeys for instance, 20 samples were investigated, whereof two were positive for H5 (10.0%), and a remarkable portion of 11 contained antibodies to H9 (55.0%). Lower numbers of H9-positives were found in the houbara bustard sample pool, in which 16 of 132 sera tested positive (12.1%), such as 3 of 20 white-bellied bustards (*Eupodotis senegalensis*; 15%), and 4 of 11 crowned cranes (*Balearica* sp.; 36.4%). Furthermore, 1 of 18 sera of greater flamingos contained antibodies to H5 (5.6%) and 4 to H9 (22.2%). An even higher antibody prevalence to H5 was found in samples of lesser flamingos, namely 20.0% (3 of 15 sera), while in 6 sera antibodies to H9 were detected (40.0%). In contrast, all samples of 23 Eurasian stone-curlews (*Burhinus oedicnemus*), 21 mallards (*Anas platyrhynchos*), 13 pigeons (family Columbidae), 13 Pharaoh eagle-owls (*Bubo ascalaphus*) and 11 silver pheasants (*Lophura nycthemera*) were antibody-negative for all AIV subtypes tested.

As shown in Table 4, seven of the wild/captive birds were positive for H5 as well as H9 antibodies. Specifically, in one ringed teal, two wild turkeys, three lesser flamingos, and one greater flamingo, antibodies to both, H5 and H9 were detected. Six of those samples were collected in 2005, and only one (a wild turkey) in 2006. In contrast, none of the falcons had antibodies to more than one AIV subtype.

TABLE 3 Detailed list of all wild/captive bird species investigated by HI for antibodies to H5N1, H7N1 and H9N2 AIV subtypes.

			Reciprocal HI titre[a] [*n*]								
Order/species	***n***	**H5/H7/H9**	**neg.**	**16**	**32**	**64**	**128**	**256**	**512**	**1024**	**Pos. [%]**
Rheiformes											
Greater rhea (*Rhea americana*)	3	H5/H7/H9	3								
Galliformes											
Lady Amherst's pheasant (*Chrysolophus amherstiae*)	1	H5/H7/H9	1								
Crested guineafowl (*Guttera pucherani*)	3	H5/H7/H9	3								
Silver pheasant (*Lophura nycthemera*)	11	H5/H7/H9	11								
Wild Turkey (*Meleagris gallopavo*)	20	H5	18	1	1						10.0
		H7	20								
		H9	9	3	3	1	2	1	1		55.0
Common pheasant (*Phasianus colchicus*)	1	H5/H7/H9	1								
Reeves's pheasant (*Syrmaticus reevesii*)	1	H5/H7/H9	1								
Anseriformes											
Mandarin duck (*Aix galericulata*)	5	H5/H7/H9	5								
Wood duck (*Aix sponsa*)	5	H5/H7	5								
		H9	4		1						20.0
Egyptian goose (*Alopochen aegyptiaca*)	2	H5/H7/H9	2								
Mallard (*Anas platyrhynchos*)	21	H5/H7/H9	21								
Domestic duck (*Anas platyrhynchos domesticus*)	1	H5/H7/H9	1								
Bar-headed goose (*Anser indicus*)	2	H5/H7/H9	2								
Canada goose (*Branta canadensis*)	2	H5/H7	2								
		H9	1	1							50.0
Barnacle goose (*Branta leucopsis*)	1	H5/H7	1								
		H9			1						100.0
Nene (*Branta sandvicensis*)	1	H5/H7/H9	1								
Ringed teal (*Callonetta leucophrys*)	5	H5	4	1							20.0
		H7	5								
		H9	4					1			20.0
Maned duck (*Chenonetta jubata*)	1	H5							1		100.0
		H7/H9	1								
Black-necked swan (*Cygnus melancoryphus*)	3	H5/H7	3								
		H9	2	1							33.3
Black-bellied whistling duck (*Dendrocygna autumnalis*)	3	H5/H7/H9	3								
Fulvous whistling duck (*Dendrocygna bicolor*)	6	H5/H7/H9	6								
White-faced whistling duck (*Dendrocygna viduata*)	1	H5/H7/H9	1								
Common shelduck (*Tadorna tadorna*)	4	H5/H7/H9	4								
Otidiformes											
Arabian bustard (*Ardeotis arabs*)	2	H5/H7	2								
		H9	1				1				50.0
Kori bustard (*Ardeotis kori*)	7	H5/H7	7								
		H9	6	1							14.3

(Continues)

TABLE 3 (Continued)

Order/species	*n*	H5/H7/H9	Reciprocal HI titre[a] [*n*]								Pos. [%]
			neg.	16	32	64	128	256	512	1024	
Houbara bustard (*Chlamydotis undulata*)	132	H5/H7	132								
		H9	116	4	2	2	1		3	4	12.1
White-bellied bustard (*Eupodotis senegalensis*)	20	H5/H7	20								
		H9	17	1	1		1				15.0
Buff-crested bustard (*Lophotis gindiana*)	2	H5/H7/H9	2								
Nubian bustard (*Neotis nuba*)	3	H5/H7/H9	3								
Little bustard (*Tetrax tetrax*)	2	H5/H7/H9	2								
Columbiformes											
Pigeon (*Columbidae*)	13	H5/H7/H9	13								
Gruiformes											
Crowned crane (*Balearica* sp.)	11	H5/H7	11								
		H9	7		1		3				36.4
Phoenicopteriformes											
Lesser flamingo (*Phoeniconaias minor*)	15	H5	12	1	1		1				20.0
		H7	15								
		H9	9	1	1	1	2	1			40.0
Greater flamingo (*Phoenicopterus roseus*)	18	H5	17		1						5.6
		H7	18								
		H9	14		4						22.2
American flamingo (*Phoenicopterus ruber*)	4	H5/H7	4								
		H9	3		1						25.0
Charadriiformes											
Eurasian stone-curlew (*Burhinus oedicnemus*)	23	H5/H7/H9	23								
Black-headed gull (*Chroicocephalus ridibundus*)	1	H5/H7/H9	1								
Great stone-curlew (*Esacus recurvirostris*)	4	H5/N7	4								
		H9	3		1						25.0
Seagull (*Laridae*)	1	H5/H7	1								
		H9		1							100.0
Ciconiiformes											
Marabou stork (*Leptoptilos crumenifer*)	1	H5/H7/H9	1								
Pelecaniformes											
Grey heron (*Ardea cinerea*)	1	H5/H7/H9	1								
Accipitriformes											
Long-legged buzzard (*Buteo rufinus*)	2	H5/H7/H9	2								
Griffon vulture (*Gyps fulvus*)	1	H5/H7	1								
		H9		1							100.0
Strigiformes											
Pharaoh eagle-owl (*Bubo ascalaphus*)	13	H5/H7/H9	13								
Psittaciformes											
Yellow-crowned amazon (*Amazona ochrocephala*)	1	H5/H7/H9	1								
Passeriformes											
White-necked raven (*Corvus albicollis*)	3	H5/H7/H9	3								

[a]Titres ≥1:16 were considered positive.

TABLE 4 Double-positive captive/wild birds with antibodies to H5 and H9 AIV subtypes.

Order/species	DFH ID	Year	HI titre H5	HI titre H9
Galliformes				
Wild turkey (*Meleagris gallopavo*)	5889	2006	1:16	1:128
	5204	2005	1:32	1:512
Anseriformes				
Ringed teal (*Callonetta leucophrys*)	4089	2005	1:16	1:256
Phoenicopteriformes				
Lesser flamingo (*Phoeniconaias minor*)	4375	2005	1:16	1:256
	4365	2005	1:32	1:32
	4376	2005	1:128	1:128
Greater flamingo (*Phoenicopterus roseus*)	4358	2005	1:32	1:32

All bird species were classified according to the International Ornithologists' Union (IOC) World Bird List version 10.1 derived from https://www.worldbirdnames.org/ioc-lists/master-list-2/.

4 | DISCUSSION

The high prevalence of antibodies to H9 found in this study (in 13.2% of falcons and in 14.4% of captive/wild birds) fits well to the observation that the H9N2 AIV subtype is widespread in poultry worldwide (Fusaro et al., 2011; Nagy et al., 2017). Although H9N2 usually causes only mild respiratory symptoms in humans, it has to be noted that all fatal AIV in humans in this century (e.g. H5N1 and H7N9) had acquired some of their gene segments from the H9N2 subtype (Cui et al., 2014; Di Liu et al., 2013; Gao et al., 2013; Guan et al., 2002; Guan et al., 1999; Pu et al., 2015). Therefore, the cocirculation of H9N2 and H5N1, especially in the Middle East and several North African countries, represents a serious threat to global health and should be closely monitored (Nagy et al., 2017; Wernery et al., 2013). On the other hand, it has also been suggested that widespread low pathogenic H9N2 prevalence in poultry may reduce the risk of severe disease caused by highly pathogenic H5N1 infections (Khalenkov et al., 2009; Negovetich et al., 2011). Therefore, a high prevalence of H9N2 subtype may be able to reduce H5N1 infections, or, just conceal them. Because similar to vaccinations, which do not prevent infection itself, but reduce visible symptoms and virus shedding, this might allow infections with H5N1 to be overlooked due to partial immunity caused by prior H9N2 challenge (Arafa et al., 2012). As a result, the highly pathogenic H5N1 virus could inadvertently spread to other animals and humans (Khalenkov et al., 2009; Negovetich et al., 2011). However, while laboratory H9N2 infections may not cause disease in birds (Khalenkov et al., 2009), natural H9N2 infections often do, especially when accompanied by stress or concurrent infections (Banet-Noach et al., 2007). Therefore, H9N2 vaccines are increasingly applied to reduce the severity of H9N2-induced diseases (Khalenkov et al., 2009). Unfortunately, the widespread application of H9N2 vaccines has increased the selection pressure on the viral genome, leading to successful antigenic adaptations, and thus reduced protection following vaccination (Pu et al., 2015).

In contrast to the H9 subtype, H5 and H7 infections appear to be much less prevalent in falcons and other birds according to our results. From all falcon samples, only one gyrfalcon hybrid (0.2%), and from all wild/captive birds, only eight (2.1%) were positive for H5 antibodies. Antibodies to H7 were not found in any of the samples above threshold. However, the susceptibility to H5 and H7 seems to differ substantially between different species. From those species with representative sample numbers, high titres of antibodies to H5 were found only in samples of lesser flamingos (20.0%) and wild turkeys (10.0%). Although H9 antibody prevalence was overall very similar in falcons and other birds, here we also found species-specific differences: 3.4% peregrine falcons, 9.5% saker falcons, 12.8% gyrfalcons and 18.2% of the gyrfalcon hybrids were positive, while a remarkable portion of 55.0% of wild turkeys, 40.0% of lesser flamingos, 36.4% of crowned cranes, 22.2% of greater flamingos, 15% of white-bellied bustards and 12.1% of houbara bustards contained antibodies to H9. Similar to the findings of Obon et al. (2009), we found the highest percentage of positive individuals among samples of lesser flamingos and wild turkeys. Moreover, of the seven birds that tested positive for H5 as well as H9 antibodies, two were wild turkeys, and three lesser flamingos. The highest antibody titres (≥1:512) were detected in wild turkeys and houbara bustards (to H9), and in a maned duck (to H5). Again in accordance with Obon et al. (2009), no specificity according to the respective orders could be observed, as the aforementioned seven species with high H9 titres belong to six different orders. However, some species seem to be more resistant to AIV in general, such as the Eurasian stone-curlew, the Pharaoh eagle-owl, pigeons and silver pheasants, which were negative for all antibody subtypes tested. Moreover, in contrast to the general perception that mallards are the number one species carrying influenza viruses, we could not detect any antibodies in this species either, suggesting that they do not play a major role as virus reservoirs.

Although AIV are repeatedly found in poultry farms in the Middle East, the transmission routes into these farms remain unclear. Due to the arid area, introduction by aquatic birds seems unlikely. In addition, the high temperatures, high ultraviolet indexes and low humidity rates are also detrimental for viral persistence in this region (Hirschinger et al., 2020). However, exposure of native birds to AIV in the area has been demonstrated by several groups (Alyas et al., 2019; Body et al., 2015; Fallah Mehrabadi et al., 2016; Fereidouni et al., 2010; Obon et al., 2009; Venkatesh et al., 2018). One possible explanation could be private bird collections, as well as breeding sites for houbara conservation efforts, which use artificial watering to create suitable habitat—also for other wild bird species. However, the opposite scenario might be more convincing, namely, sporadic spillover from local poultry farms to wild birds. The direct and indirect contact opportunities between wild and captive birds provided by aviaries and breeding sites definitely constitute a possible transmission route (Hirschinger et al., 2020). In addition, three major migratory flyways are partly overlapping above the Middle East, namely, the Black Sea–Mediterranean, the East Africa–West Asia

and the Central Asian flyways. Therefore, millions of migratory birds regularly fly over this region, possibly coming into contact with resident and domestic birds (Nagy et al., 2017). However, it is still debated whether migratory birds are the main reservoir spreading HPAIV to resident and domestic birds, or if domestic fowl and poultry are the reservoir, and wild species are only sporadically infected (Khalenkov et al., 2009).

A study performed in Bangladesh found only minimal prevalence of AIV in migratory waterfowl (1.7%). In contrast, at six different retail markets selling live birds (mainly chickens), influenza A was detected in up to 77.9% of the oropharyngeal swab samples, and in up to 61.9% of faeces, water troughs and similar sources (Negovetich et al., 2011). As in the present study, the vast majority of positive samples in Bangladesh contained the subtype H9 (94.2%), the few remaining were H1, H3, H4, H5 and H10. The fact that AIV have also been found in ducks at these markets suggests that multispecies live markets provide the perfect conditions for interspecies transmission and increase the risk of reassortment between different virus subtypes. Interestingly, all of the sampled birds appeared healthy, including those that were positive for subtype H5N1 (Negovetich et al., 2011), indicating that infections mostly remain unrecognised. Another study from Bangladesh testing 626 birds on live bird markets showed a prevalence of AIV in pigeons of 17.36%, and in quail of 38.75%, with a majority of H9 in quail (17.92%). Vendors purchasing waterfowl from a wholesale market instead of farms, and mixing healthy and sick birds as well as new birds with unsold birds, had a significantly higher risk to be positive for AIV. In contrast to Negovetich et al. (2011), Islam et al. (2022) found the likelihood of AIV detection to be 4.19 times higher in sick and deceased birds compared to healthy ones. They concluded that proper hygienic practices were not maintained and recommended improving biosecurity practices at live bird markets (Islam et al., 2022). A study from China investigating 742,005 environmental samples related to poultry and wild birds during 2014—2018 found significantly higher AIV rates in live poultry markets (30.42%) and slaughterhouses (22.96%) compared to samples collected from poultry farms (3.26%), backyards (3.44%) and wild bird habitats (1.1%), with a proportion of H9N2 of 46.9% among all samples (Bo et al., 2021). A surveillance study of AIVs in live bird markets in China from 2013 to 2019 testing 29,895 samples, found an overall AIV rate of 9.7%, again with H9 being the most predominant subtype (Liu et al., 2022). The widespread prevalence of H9N2 is also of concern because isolates of this subtype mostly possess the Q226L mutation in their receptor-binding site, which confers specificity to human SAα2,6-Gal-linked receptors (Alyas et al., 2019; Matrosovich et al., 2001; Negovetich et al., 2011; Wernery et al., 2013). This mutation, especially in combination with the potential for airborne transmissibility (Shi et al., 2010), substantially elevates the risk of infection for humans working at or visiting live bird markets (Negovetich et al., 2011).

The complete genome sequencing after an H9N2 outbreak in a chicken farm in Dubai in 2015 showed no virulent elements in the viral genome, but identified several other mutations, which possibly contributed to the outbreak (Lau et al., 2016). A study performed in 2013 on birds used for falconry in the UAE found multiple substitutions in the H9N2 genome conferring specificity to human receptors (Wernery et al., 2013). Potentially infected birds used to train falcons are often smuggled into the country, thereby enabling the dissemination of these viruses to other birds and humans. The ability of H9N2 viruses to exchange gene segments, thereby creating strains that may be lethal for humans, should remind us of the possible consequences of using potentially infected birds for falconry (Wernery et al., 2013). A study investigating an HPAIV outbreak in hunting falcons and other captive wild birds in Dubai in 2014 revealed subtype H5N1 as causative agent. Genetic analyses of these viruses indicated reassortants between H5N1 and H9N2 from Southeast Asia, probably acquired during a recent hunting trip to Central Asia (Naguib et al., 2015). Another study on the risk of AIV in falconry carried out in Germany from 2006 through 2008 found AIV RNA in roughly 4% of prey birds, but neither RNA nor antibodies in falcons. Moreover, albeit all serum samples of the falconers were positive for influenza A virus antibodies, they all remained negative for H5, H7 and H9 antibodies (Kohls et al., 2011). Therefore, it can be assumed that there is a limited risk for falconers in Germany to get infected with AIV. A study performed on captured birds of prey in South Africa in 2018 found three out of 24 raptors (12.5%) positive for IAVs, with viral RNA detected in both oropharyngeal and cloacal swabs. Apart from one sample that was positive for H5 (4.1%), all other samples were negative for subtypes H5, H7 and H9 (El Zowalaty et al., 2022). However, another study performed on captive falcon hybrids demonstrated that these birds are highly susceptible to H5N1 infection by ingestion of infected prey (Bertran et al., 2012). Thus, it seems falconry does pose a certain risk to birds and humans, and the source and health status of the used birds should be controlled carefully.

Due to the decline of the houbara bustard populations in the wild, many breeding programs have been established across the Middle East. However, the release of captive-bred birds potentially threatens wild populations with disease transmission (Bailey et al., 1996). Therefore, disease surveillance must be an integral part of reintroduction programs (International Union for Conservation of Nature, Species Survival Commission IUCN/SSC, 2013), and the vaccination of the birds before release should be considered. An H5N1 vaccination trial in houbara bustards has demonstrated successful immunisation in 84% of birds after 60 days. Moreover, the absence of adverse reactions has indicated its safety and potential for application in other species (Wernery et al., 2006). Also another vaccination study that applied a combination of two different inactivated vaccines (H5N2 and H9N2), performed in the UAE on 11 different bird species, showed a very high success rate in terms of antibody generation (94%) and the lack of any adverse reactions (Obon et al., 2007).

This study was carried out on samples collected between 2003 and 2006, which is the main limitation of the study. Due to personal reasons we were not able to publish earlier. Nonetheless the presented data are of relevance up to today, as we tried to show in the discussion section, and publications on this topic from the Arabian Peninsula are scarce. Given the current unprecedented AIV (H5N1) outbreaks worldwide (with the exception of Australasia and Antarctica), resulting in huge economic losses to the poultry industries and also increasing

reports of infections in various species of mammals including humans (Leung et al., 2023), even past reference data may be of value to the scientific community.

5 | CONCLUSIONS

Several subtypes of AIV have been detected in the UAE, including H7N1, H9N2 and H7N3, whereby the latter had been the only one exerting highly pathogenic effects in chickens (Kent et al., 2006; Manvell et al., 2000; Obon et al., 2009). However, the findings of H5N1 in Saudi Arabia and Kuwait, and H7N3 in Pakistan, have also raised concerns in the UAE due to the close proximity (Abbas et al., 2010; Marjuki et al., 2009; Obon et al., 2009). In the present study, only minimal levels of antibodies to H5 were detected, and none to H7. From 592 falcons, only one was positive for H5 antibodies (0.2%), and out of 383 wild/captive birds sampled, eight were positive for antibodies to H5 (2.1%). These results indicate that infections with H5N1 or H7N1 are very rare in falcons as well as other birds, suggesting that the contact with these birds should not be of major concern. In contrast, the vast majority of severe influenza cases seem to arise in crowded poultry farms and live bird markets. One possible attempt to limit the further spread of AIV may be stricter hygiene standards, as it has been shown that a lack of hygiene and biosecurity measures, especially regarding the disposal of dead birds, but also concerning the transport of manure and feed, largely impacts the risk for AIV dissemination (Fallah Mehrabadi et al., 2016; Islam et al., 2022).

AUTHOR CONTRIBUTIONS

Conceptualisation: T.A.B. and N.N. Methodology: T.A.B., N.J., P.W., H.L., S.J. and N.N. Software: P.W. Validation: T.A.B., X.L. and N.N. Formal analysis: N.J., H.L. and P.W. Investigation: N.J., H.L. and S.J. Resources: T.A.B. and N.N. Data curation: N.J., H.L., S.McK. and D.O'D. Writing – original draft preparation: N.J. and P.W. Writing – review and editing: P.W., T.A.B., X.L. and N.N.; Visualisation: N.J. and P.W. Supervision: T.A.B. and N.N. Project administration: T.A.B. and N.N. Funding acquisition: none. All authors have read and agreed to the published version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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This research received no external funding.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to. Ethical review and approval were waived for this study because all samples originated either from the serum depository of Dubai Falcon Hospital or have been submitted from private persons or zoos. All serum samples were submitted for diagnostic purposes including AIV serology.

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