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Transmission of highly pathogenic avian influenza H5N1 virus in Pekin ducks is significantly reduced by a genetically distant H5N2 vaccine

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ABSTRACT

Domestic ducks play an important role in the epidemiology of H5N1 avian influenza. Although it is known that vaccines that have a high homology with the challenge virus are able to prevent infection in ducks, little is yet known about the ability of genetically more distant vaccines in preventing infection, disease, and transmission. Here we study the effect of a widely used H5N2 vaccine (A/Chicken/Mexico/232/94/CPA) on the transmission of H5N1 virus (A/Chicken/China/1204/04) in ducks. The quantitative analyses show that despite the low level of homology between the virus and vaccine strain transmission was significantly reduced two weeks after a single or double vaccination. Mortality and disease rates were reduced markedly already one week after a single vaccination.

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Introduction

Wild aquatic birds are the natural host species for avian influenza (Webster et al., 1992; Alexander, 2000). Most highly pathogenic avian influenza (HPAI) viruses replicate but do not cause disease symptoms in ducks (Alexander et al., 1978, 1986; Westbury et al., 1979; Wood et al., 1985, 1995). In accordance with this finding, early Asian HPAI H5N1 viruses were non-pathogenic to ducks. However, since 2002 several H5N1 strains emerged that induce severe disease and mortality, while other H5N1 strains still cause asymptomatic infections (Sturm-Ramirez et al., 2004, 2005; Hulse-Post et al., 2005; Kishida et al., 2005; Tian et al., 2005; Webster et al., 2006b; Beato et al., 2007; Middleton et al., 2007). Most HPAI viruses can be transmitted from infected to uninfected ducks, as has been shown in experimental studies (Alexander et al., 1978, 1986; Westbury et al., 1979; Chen et al., 2004; Sturm-Ramirez et al., 2004, 2005; Beato et al., 2007; Pantin-Jackwood et al., 2007). In the group of Asian H5N1 viruses there does not seem to be a clear correlation between the pathogenicity and the ability to spread from duck to duck. In fact, transmission is observed in strains that cause subclinical infections as well as in strains that cause severe disease and mortality (Sturm-Ramirez et al., 2004, 2005; Hulse-Post et al., 2005; Beato et al., 2007; Pantin-Jackwood et al., 2007).

Domestic ducks play an important role in the epidemiology of HPAI H5N1 viruses. It has been shown that free-ranging ducks act as a reservoir of H5N1 avian influenza viruses (Songserm et al., 2006), and are a risk factor for the presence of H5N1 virus infections of domestic poultry (Gilbert et al., 2006, 2008). Since not all H5N1 infections are symptomatic, the chance that infections in adult ducks are not detected is substantial. This was illustrated by Kwon et al. (2005), who showed that an H5N1 infection in adult breeder ducks was only detected after the 9 day old offspring showed signs of infection.

Vaccination is a potentially attractive tool for the prevention and control of avian influenza outbreaks. At present, vaccination against HPAI H5N1 is practiced in several countries e.g. Indonesia, People's Republic of China and Vietnam (OIE, 2008b). Vaccines based on different seed viruses are used, with different antigenic homology with the circulating field strains. In chickens it has been shown that the homology between the hemagglutinin of the vaccine strain and the challenge strain is an important factor in the reduction of virus shedding (Swayne et al., 1999, 2000a).

Experimental studies investigating the effect of vaccination in ducks show that virus excretion is significantly reduced after vaccination (Tian et al., 2005; Webster et al., 2006a; Beato et al., 2007; Middleton et al., 2007). In fact, in most studies no virus could be isolated from the

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Table 1
Transmission of H5N1 in unvaccinated ducks

	D1[a]	D2	D3	D4	D5	D6	D7	D8	D9	D10	Symptoms
I	+/-	+/+	+/+	+/-	-/-	-/-	-/-	-/-	-/-	-/-	a
I	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-
I	+/+	+/+	+/+	+/+	†						b
I	+/-	+/-	+/+	+/+	+/-	-/+	-/-	-/-	-/-	-/-	a,c
S	nd	+/-	+/-	+/+	+/+	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/+	+/-	-/-	-/-	-/-	-/-	-/-	-/-	a
S	nd	+/-	+/-	+/+	+/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	-/-	+/+	+/+	+/-	+/-	+/-	-/-	-/-	-/-	a
S	nd	+/-	+/-	+/+	+/-	+/-	-/-	-/-	-/-	-/-	-
I	+/-	+/-	+/+	+/+	+/+	+/-	-/-	-/-	-/-	-/-	a
I	+/+	+/+	+/+	+/+	+/-	-/-	-/-	-/-	-/-	-/-	-
I	+/+	+/+	+/+	+/-	+/+	†					b
I	+/-	+/+	+/+	+/+	+/-	+/-	-/-	-/-	-/-	-/-	a
I	+/-	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	a,c
S	nd	+/-	+/-	+/+	+/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/+	+/+	+/+	+/+	-/-	-/-	-/-	-/-	-
S	nd	+/+	+/+	+/+	+/+	-/-	-/-	-/-	-/-	-/-	a
S	nd	+/-	+/+	+/+	+/+	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-

Pekin ducks were inoculated with A/Chicken/China/1204/04 H5N1 virus.
Two duplicate experiments were performed.
[a]Day after challenge; I, inoculated bird; S, contact bird; nd, not determined; †, duck died; *x*/*y*, results of the virus isolation in ECE's of the tracheal swab (*x*) and the cloacal swab (*y*); grey box, trachea and/or cloacal swab was positive in the virus isolation; a, conjunctivitis; b, bird died; c, depressed; –, no symptoms were observed.

Table 3
Transmission of H5N1 in ducks two weeks after a single vaccination

	D1[a]	D2	D3	D4	D5	D6	D7	D8	D9	D10	Symptoms
I	-/-	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	d
I	-/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	-/-	+/-	+/+	+/+	+/-	-/-	-/-	-/-	-/-	-
S	nd	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	a
I	+/-	+/-	+/+	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	a,d
S	nd	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	-/-	+/-	+/+	+/+	-/-	-/-	-/-	-/-	-/-	-

Pekin ducks were inoculated with A/Chicken/China/1204/04 H5N1 virus, two weeks after a single vaccination with an inactivated H5N2 vaccine (A/Chicken/Mexico/232/94/CPA). Two duplicate experiments were performed.
[a]Day after challenge; I, inoculated bird; S, contact bird; nd, not determined; *x*/*y*, results of the virus isolation in ECE's of the tracheal swab (*x*) and the cloacal swab (*y*); grey box, trachea and/or cloacal swab was positive in the virus isolation; a, conjunctivitis; d, swollen oropharynx; –, no symptoms were observed.

swabs at all. But it should be noticed that in most of these studies the homology between vaccine and virus strains is high, and that not all currently used vaccines have this high homology with the recent Asian H5N1 viruses. For this reason we are interested in the effectiveness of vaccines that are currently used and that have a larger genetic and antigenic distance from the Asian H5N1 viruses.

In this paper we report results of transmission experiments that were carried out to quantify the effectiveness of vaccination with a widely used H5N2 vaccine (A/Chicken/Mexico/232/94/CPA) in reducing disease and transmission of H5N1 virus (A/Chicken/China/1204/04) in Pekin ducks. In a transmission experiment a number of infected ducks is housed together with a number of uninfected ducks, and the infection chain is monitored on a regular basis. In our experiments disease symptoms and excretion of virus were monitored daily, while the antibody response was determined weekly. The aim of transmission experiments is to obtain estimates of the basic reproduction ratio (R), which is defined as the number of secondary infections that would

Table 2
Transmission of H5N1 in ducks one week after a single vaccination

	D1[a]	D2	D3	D4	D5	D6	D7	D8	D9	D10	Symptoms
I	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	-/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	-/-	-/-	-/-	+/-	+/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-
I	+/+	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	+/+	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	a
I	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	-/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
I	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/-	-/-	+/-	+/-	-/-	-/-	-/-	-/-	-/-	-
S	nd	+/+	+/+	+/-	-/-	-/-	-/-	-/-	-/-	-/-	a

Pekin ducks were inoculated with A/Chicken/China/1204/04 H5N1 virus, one week after a single vaccination with an inactivated H5N2 vaccine (A/Chicken/Mexico/232/94/CPA). Two duplicate experiments were performed.
[a]Day after challenge; I, inoculated bird; S, contact bird; nd, not determined; *x*/*y*, results of the virus isolation in ECE's of the tracheal swab (*x*) and the cloacal swab (*y*); grey box, trachea and/or cloacal swab was positive in the virus isolation; a, conjunctivitis; –, no symptoms were observed.

Table 4
Transmission of H5N1 in ducks two weeks after a double vaccination

	D1[a]	D2	D3	D4	D5	D6	D7	D8	D9	D10	Symptoms
I	-	-	-	-	-	-	-	-	-	-	-'
I	-	-	-	+/-	-	-	-	-	-	-	-'
I	-	-	-	-	+/-	-	-	-	-	-	-'
I	-	-	-	-	-	-	-	-	-	-	-'
S	nd	+/-	+/-	+/+	+/-	+/-	-	-	-	-	a
S	nd	-	-	-	-	-	-	-	-	-	-'
S	nd	-	-	-	-	-	-	-	-	-	-'
S	nd	-	-	-	-	-	-	-	-	-	-'
S	nd	-	-	-	-	-	-	-	-	-	a
I	-	-	-	-	-	-	-	-	-	-	-'
I	+/-	+/-	+/-	+/-	+/-	-	-	-	-	-	-'
I	-	-	-	-	-	-	-	-	-	-	-'
I	-	-	-	-	-	-	-	-	-	-	-'
I	+/-	+/-	+/-	+/-	-	-	-	-	-	-	-'
S	nd	-	-	-	-	-	-	-	-	-	-'
S	nd	-	-	-	-	-	-	-	-	-	-'
S	nd	-	-	-	-	-	-	-	-	-	-'
S	nd	-	-	-	-	-	-	-	-	-	-'
S	nd	-	-	-	-	-	-	-	-	-	-'

Pekin ducks were inoculated with A/Chicken/China/1204/04 H5N1 virus, two weeks after a double vaccination with an inactivated H5N2 vaccine (A/Chicken/Mexico/232/94/CPA). Two duplicate experiments were performed.
[a]Day after challenge; I, inoculated bird; S, contact bird; nd, not determined; –, swab was negative in the RRT-PCR; *x*/*y*, results of the virus isolation in ECE's of the tracheal swab (*x*) and the cloacal swab (*y*); grey box, trachea and/or cloacal swab was positive in the virus isolation; a, conjunctivitis; –', no symptoms were observed.

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