

Do contrasting patterns of migration movements and disease outbreaks between congeneric waterfowl species reflect differing immunity?

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Abstract

Long-distance migrations influence the dynamics of host-pathogen interactions and understanding the role of migratory waterfowl in the spread of the highly pathogenic avian influenza viruses (HPAIV) is important. While wild geese have been associated with outbreak events, disease ecology of closely related species has not been studied to the same extent. The swan goose (*Anser cygnoides*) and the bar-headed goose (*Anser indicus*) are congeneric species with distinctly different HPAIV infection records; the former with few and the latter with numerous records. We compared movements of these species, as well as the more distantly related whooper swan (*Cygnus cygnus*) through their annual migratory cycle to better understand exposure to HPAIV events and how this compares within and between congeneric and non-congeneric species. In spite of their record of fewer infections, swan geese were more likely to come in contact with disease outbreaks than bar-headed geese. We propose two possible explanations: i) frequent prolonged contact with domestic ducks increases innate immunity in swan geese, and/or ii) the stress of high-elevation migration reduces immunity of bar-headed geese. Continued efforts to improve our understanding of species-level pathogen response is critical to assessing disease transmission risk.

Introduction

Long-distance migrations in wildlife co-determine the dynamics of host-pathogen interactions (Altizer *et al.*, 2011). The role migration plays in the host-pathogen relationship can be extremely complex, with migration presenting an opportunity for a disease to spread across a landscape while also potentially reducing prevalence via death during travel or allowing healthy individuals to separate from infected individuals or regions (Altizer *et al.*, 2011; Risely *et al.*, 2018). Migration can even be an important part in the life cycle of a pathogen due to reduced immune function (Owen & Moore, 2008; Hawley & Altizer, 2011) and increased exposure of the host across the migratory route (Fritzsche & Hoyer, 2016; Leung & Koprivnikar, 2016), or by animals being together in dense congregations thereby facilitating disease transmission (Hill



et al., 2012; Fritzsche & Hoye, 2016; van Dijk *et al.*, 2018). However, despite the complex and compelling relationship between wildlife migrations and the potential pathogens these animals carry, relatively few studies have examined how annual migration movements affect the transmission and evolution of pathogens within host populations (Hall *et al.*, 2014; Verhagen *et al.*, 2015). A prime example of this dearth of information is found in wild waterfowl whose migration is a well-known ecological phenomenon; yet, the relationship between migration and disease spread is not well understood.

Traditional amplification routes of avian influenza viruses include direct or indirect transmission of the non-lethal, low-pathogenic avian influenza virus (LPAIV) from wild bird reservoirs to highly-dense populations such as farmed poultry. This transmission is often facilitated by agricultural practices with low biosecurity (Takekawa *et al.*, 2010a and b; Fearnley, 2015), such as grazing domestic ducks in marshes where they can come in contact with migratory wild birds. This viral flow is demonstrated by the amplified infection prevalence of locally circulating LPAIVs observed concurrent with the arrival of migratory waterfowl (Lisovski *et al.*, 2018; Verhagen *et al.*, 2015). Once introduced to highly concentrated poultry herds in domestic facilities, LPAIVs can easily mutate into a highly pathogenic virus, which can have dramatic impacts on affected poultry farms (Wallace, 2016).

The emergence of the Asian lineage HPAI H5N1 virus marked the evolution of the highly pathogenic avian influenza viruses (HPAIV) spill-over from poultry to wild birds and the environment. For instance, the HPAIV H5N1 outbreak at Qinghai Lake in 2005 killed over 6000 wild migratory waterfowl, more than 90% of which were bar-headed geese (*Anser indicus*) (Chen *et al.*, 2005; Liu *et al.*, 2005). Subsequent research has suggested that, much like the introduction of LPAIV from wild birds to domestic poultry, spill-over of HPAIV from domestic poultry to wild birds is likely facilitated by agricultural practices (Hénaux & Samuel, 2011; Prosser *et al.*, 2016; Stallknecht *et al.*, 1990) that enable co-occurrence of the virus and its avian hosts in wetlands (Prosser *et al.*, 2016; Takekawa *et al.*, 2010a). Thus, areas with high concentrations of domestic ducks and geese as well as migratory waterfowl, such as southeast China (Prosser *et al.*, 2013), are especially prone to outbreaks of HPAIV and can serve as disease hotspots (Gilbert *et al.*, 2012; Cappelle *et al.*, 2014). However, once HPAIV spill-over into the environment, it is not limited to these high-risk areas. Research indicates that some waterfowl species can migrate while infected with HPAIV (Hill *et al.*, 2012), which strengthens the potential for long-distance dispersal (Altizer *et al.*, 2011; Verhagen *et al.*, 2015).

Though previous work has addressed many questions regarding the spatial-temporal correlations between waterfowl migration and HPAIV outbreaks (Newman *et al.*, 2009; Si *et al.*, 2009; Verhagen *et al.*, 2014), phylogenetic relationships among outbreaks (Tian *et al.*, 2015; Xu *et al.*, 2016), and outbreak drivers (Gilbert *et al.*, 2007; Prosser *et al.*, 2013), there are no studies we are aware of comparing HPAIV outbreak patterns in congeneric migratory waterfowl species. The swan goose (*Anser cygnoides*) and the bar-headed goose provide an ideal opportunity for examining avian influenza in congeners as these species both breed in Mongolia (Batbayar *et al.*, 2013) and co-occur in some areas but follow separate migration routes (Batbayar, 2013). During the autumn migration, swan geese use northeast China and the Yalu River Estuary as important stopover sites (Batbayar *et al.*, 2013) on their way to over-wintering in the Yangtze River lowlands via

the East Asian-Australasian Flyway. In contrast, the bar-headed geese stopover at Qinghai Lake and wetlands on the Qinghai Plateau in the Central Asian Flyway (Takekawa *et al.*, 2017) before migrating to southern Tibet or India. Additionally, while passive and active surveillance indicate that swan geese are generally infected infrequently and in low numbers (Kou *et al.*, 2009; Welte & Terán, 2004), bar-headed geese have been regularly documented in HPAIV outbreaks from 2004-2017. This suggests species differences, either with respect to exposure to, or immunity against, HPAIV (Welte & Terán, 2004; Chen *et al.*, 2005; Takekawa *et al.*, 2010b). In this study, we compare migratory movements of the bar-headed geese and the swan geese and examine HPAIV outbreak patterns along their migration routes. We also contrast their movements to those of two whooper swan (*Cygnus cygnus*) populations to: i) provide comparison with a different genus of waterfowl that migrates along comparable habitats; and ii) examine whether HPAIV outbreak patterns between and within waterfowl species are correlated with the variable densities of domestic ducks. We discuss mechanisms that may contribute to differences in outbreak patterns and transmission, such as migration strategies and immunity.

Materials and methods

Tracking data

We obtained global positioning system (GPS) data tracking bar-headed geese and swan geese from the U.S. Geological Survey (USGS) and the Food and Agriculture Organization of the United Nations (FAO). In addition, we acquired data for swan geese from the Department of Earth System Science at Tsinghua University, Beijing, China and included movement data of two whooper swan populations: one migrating between Mongolia and South Korea (USGS-FAO) and the other between Russia and Japan (Shimada *et al.*, 2014). These different migration corridors overlap with high and low poultry density areas, respectively, which enables within-species comparison.

The USGS-FAO information included a total of 18 swan geese, 38 bar-headed geese, and 10 whooper swans captured in overwintering and breeding areas (Table 1); the Tsinghua University sample 44 swan geese marked in overwintering and breeding areas (Xu *et al.*, 2016); and the Shimada *et al.* (2014) data concerned a total of 47 whooper swans captured in eastern Hokkaido and north-eastern Honshu, Japan. The GPS and ARGOS platform transmitting terminals (see Table 1 for further information) were programmed to record locations at 2-hour intervals for swan geese and whooper swans and at 4-hour intervals for bar-headed geese. Additional information can be found in the Table 1 and in previous papers (Newman *et al.*, 2009, 2012; Batbayar *et al.*, 2013; Shimada *et al.*, 2014; Xu & Si, 2019; Xu *et al.*, 2019).

Migration route estimations

We used dynamic Brownian Bridge Movement Models (dBBMM) to measure utilization distributions (UD) of the tracked populations (Kranstauber *et al.*, 2012). The dBBMM assumes heterogeneous GPS tracks and thereby estimates UD with a sliding window of GPS locations for detecting behavioural changes. We used a resolution of 10 km with a sliding window encompassing 23 locations with a margin of 11 locations and a location error of 23

m (Palm *et al.*, 2015). We set the time step at 8 locations for swan geese and whooper swans and at 4 locations for bar-headed geese covering a 16-h period.

Because tracking durations varied among individuals, we weighted their individual UD by multiplying all raster values by the number of tracking days. Population-level UDs were calculated from the sum of weighed individual UDs, and we generated 90% cumulative probability contours to circumscribe their main use areas including breeding, stopover, and wintering areas (Si *et al.*, 2018; Xu *et al.*, 2019). We used 99% cumulative probability contours to represent migration routes (Palm *et al.*, 2015).

Because original tracking data for the Russia-Japan whooper swans were not available, we extracted coordinates for the main areas of wintering, stopover, and breeding sites from published maps (Shimada *et al.*, 2014) via geo-referencing and created buffer zones around each of these geo-referenced sites with a radius of 32.5 km, *i.e.* an average maximum foraging distance for waterfowl (Johnson *et al.*, 2014).

Poultry density measurements

We obtained densities of domestic ducks from the Livestock Geo-Wiki (<https://livestock.geo-wiki.org/home-2/>). To evaluate the differences among migratory populations and their contact probability with poultry, we summarized densities of domestic ducks and chickens from each raster cell in sites used along their migration routes, derived from tracking data from 2004-2017. Differences in poultry densities in areas of different migratory populations were tested with Bonferroni corrected post-hoc tests (Dunn, 1961).

Highly pathogenic avian influenza viruses outbreak assessments

We obtained confirmed HPAIV outbreaks from 2004-2017 through EMPRES-i (Welte & Terán, 2004). We assumed an outbreak window of 30 days (*i.e.*, where the outbreak observation date is the median date) during which the virus may be transmitted to wild migratory birds that visit the outbreak areas with an incuba-

tion period of 21 days plus a disinfection period of 9 days (Si *et al.*, 2009). We extracted GPS locations for tracked individuals during each outbreak window and examined the distribution of distances between these locations and HPAIV outbreaks. Differences among cumulative distributions were tested with a Kolmogorov-Smirnov test (Frank & Massey, 1951). We ran the analysis in R 3.4.3 (R Development Core Team, 2016) and QGIS 2.18 (QGIS Development Team, 2015).

Results

The marked swan geese bred in north-eastern Mongolia used the Yalu River Estuary at the border of China and North Korea as a stopover site and overwintered in the Yangtze River Lowlands of southern China including Poyang Lake. Bar-headed geese bred in north-western Mongolia and migrated over the Gobi Desert and the Qinghai-Tibetan Plateau. Eight of the 36 bar-headed geese crossed the Himalayas and overwintered in India, whereas the rest of the marked bar-headed geese overwintered near Lhasa, China. The breeding grounds for the population of whooper swans marked by the USGS-FAO were near the Mongolia-Russia border and they migrated to southern South Korea for overwintering. The other whooper swan population was located in north-eastern Russia and southern Japan (Figure 1).

There were no HPAIV outbreaks concerning swan geese in the EMPRES-i database between 2004 and 2017, but 11 HPAIV outbreaks in bar-headed geese and 37 in whooper swans (Table 2). The HPAIV outbreaks in bar-headed geese occurred in Mongolia, around Qinghai Lake, and in the Lhasa River Valley, while HPAIV outbreaks in whooper swans mainly occurred in Japan (Figure 1C).

There were fewer HPAIV outbreaks, *i.e.* outbreaks in domestic and wild birds along the migration route for swan geese compared with the other species. A total of 20 HPAIV outbreaks occurred along the migratory route of the swan geese, whereas 48 outbreaks occurred along the migration route of the bar-headed geese (Table 2). 67 outbreaks occurred along the migratory route of the whooper

Table 1. Summary of marked bird population data.

Population of individuals	Number duration (days)	Tracking capture	Year of data	Capture location	GPS transmitter	Data source
Swan goose <i>Anser cygnoides</i>	18	1211	2006, 2008	Khaichiin Tsagaan Lake, Khorin Tsagaan Lake and Khokh Lake, Mongolia	Solar-powered Argos-GPS platform transmitter terminals*	USGS/FAO
Swan goose <i>Anser cygnoides</i>	44	435	2015, 2016	Hulun Lake, China	GPS-GSM solar-powered loggers ^o	Tsinghua University
Whooper swan <i>Cygnus cygnus</i>	10	820	2006	Khorin Tsagaan Nuur and Delger Tsagaan Lake, Mongolia	Solar-powered Argos-GPS platform transmitter terminals*	USGS/FAO
Whooper swan <i>Cygnus cygnus</i>	47	1380	2009, 2010	Lake Kussharo, Lake Izunuma-Uchinuma	Solar- and battery-powered Argos-GPS platform transmitter terminals*	Shimada <i>et al.</i> (2014)
Bar-headed goose <i>Anser indicus</i>	38	788	2008, 2009	Terkhiin Tsagaan Lake, Mongolia, Chilika Lake, East India, Koonthankulum Bird Sanctuary, South India	Solar-powered Argos-GPS platform transmitter terminals*	USGS/FAO

*Platform transmitting terminals: Microwave Telemetry, Inc., Columbia, MD, USA; ^oGPS-GSM, Global Positioning System - Global System for Mobile Communications. The transmitters were IBIS series, Ecotone Telemetry, Gdynia, Poland and necked HQNG series, Hunan Global Messenger Technology Co. Ltd., Xiangtan, China; The GPS and ARGOS transmitters were programmed to record GPS locations at 2-hour intervals for swan geese and whooper swans and 4-hour intervals for bar-headed geese.

Swans from Mongolia, and 44 outbreaks occurred in the sites of whooper swans in Russia and Japan (Table 2).

Swan geese were closer to outbreak locations than bar-headed geese and whooper swans within a radius of 500 km around outbreak events (Figure 2D). Densities of domestic ducks in both the stopover, breeding and wintering sites and migration routes of the swan geese were also higher than those for bar-headed geese (Figure 2A and B). Densities of domestic ducks in the 90% cumulative probability contours of the Mongolia-South Korean whooper swan population was higher compared to those in Russia and Japan (Figure 2C), but the number of outbreaks was higher for the Russia-Japan population (Table 2).

Discussion and conclusions

We compared HPAIV outbreak patterns between two congeneric species, the swan geese and the bar-headed geese and found that there were no recorded HPAIV outbreaks in the former but multiple outbreaks in latter. Contrary to our expectations, swan geese were found closer to outbreak areas than bar-headed geese during HPAIV outbreaks. Also, areas used by swan geese had significantly higher duck densities than areas used by bar-headed geese that were often reported in outbreaks. Although the swan geese were more likely to be present in HPAIV outbreak areas during migration, they had a lower chance of being infected with

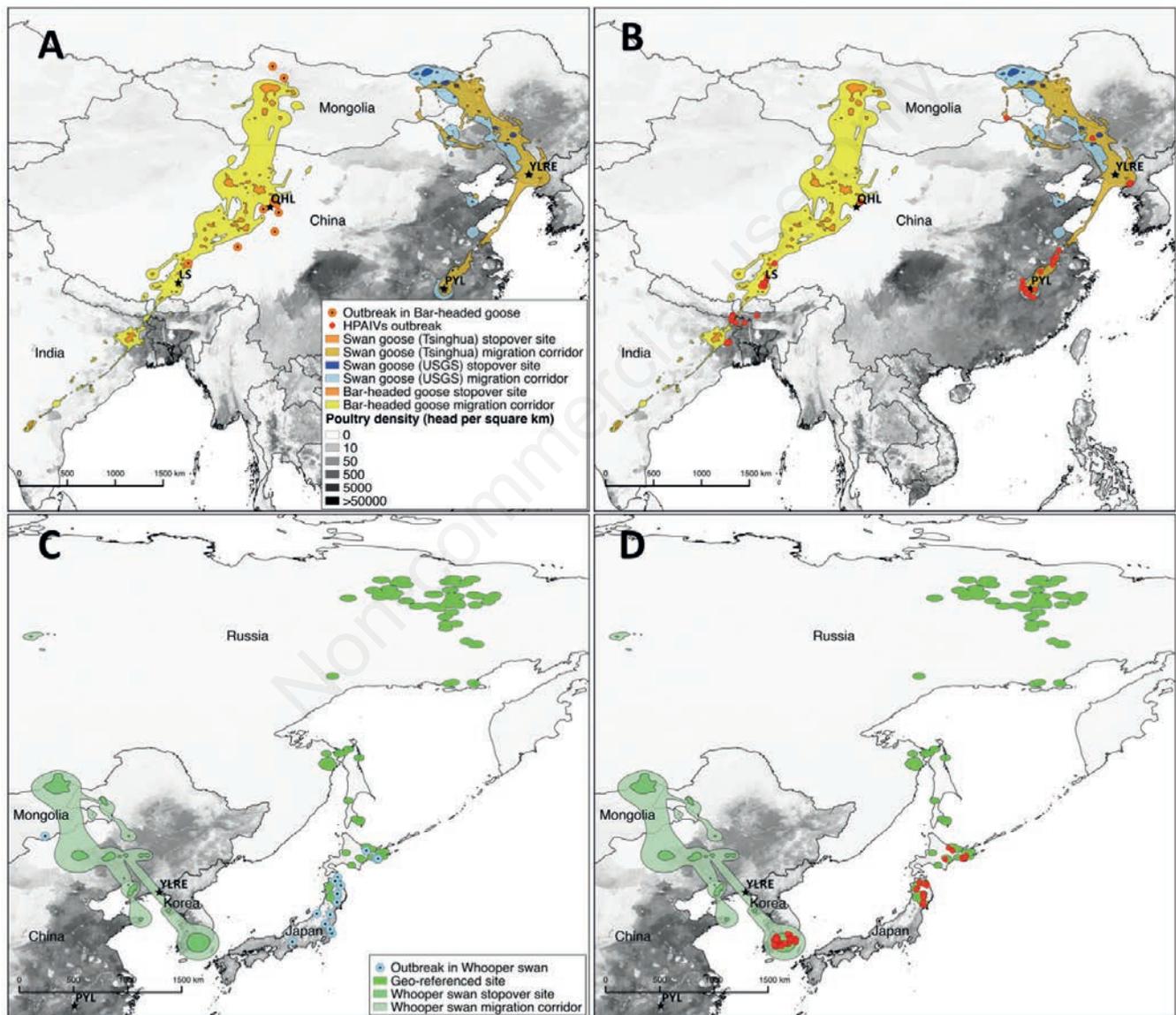


Figure 1. Primary stopover sites, migration corridors for bar-headed geese and swan geese. The swan geese are from different marked populations (A and B) overlaid on poultry densities (grey shading) where darker shades indicate higher densities. For comparison, relationship of domestic poultry densities with two whooper swan populations are shown (C and D). Black stars represent important stopover sites for the migratory geese, including Qinghai Lake (QHL), Yalu River Estuary (YLRE), Poyang Lake (PYL), and Lhasa region (LS). Orange circles represent HPAIV outbreaks in bar-headed geese. Blue circles represent HPAIV outbreaks in whooper swans. Red dots are the confirmed HPAIVs outbreaks in wild birds and domestic birds.

HPAIVs. However, the bar-headed geese were less likely to contact HPAIVs outbreaks during migration but had multiple HPAIV outbreaks. We postulate two possible explanations for this: i) frequent contact and long contact history with domestic ducks might cause greater levels of innate immunity in swan geese; and/or ii) the high elevation Himalayan migration of bar-headed geese could

compromise their immunity resulting in greater vulnerability to HPAIV infection.

Firstly, wild birds that have frequent contacts with domestic birds are less often found in outbreaks because they may have greater levels of immunity from frequent exposure to poultry (Brown *et al.*, 2008; Nemeth *et al.*, 2013; Pantin-Jackwood *et al.*,

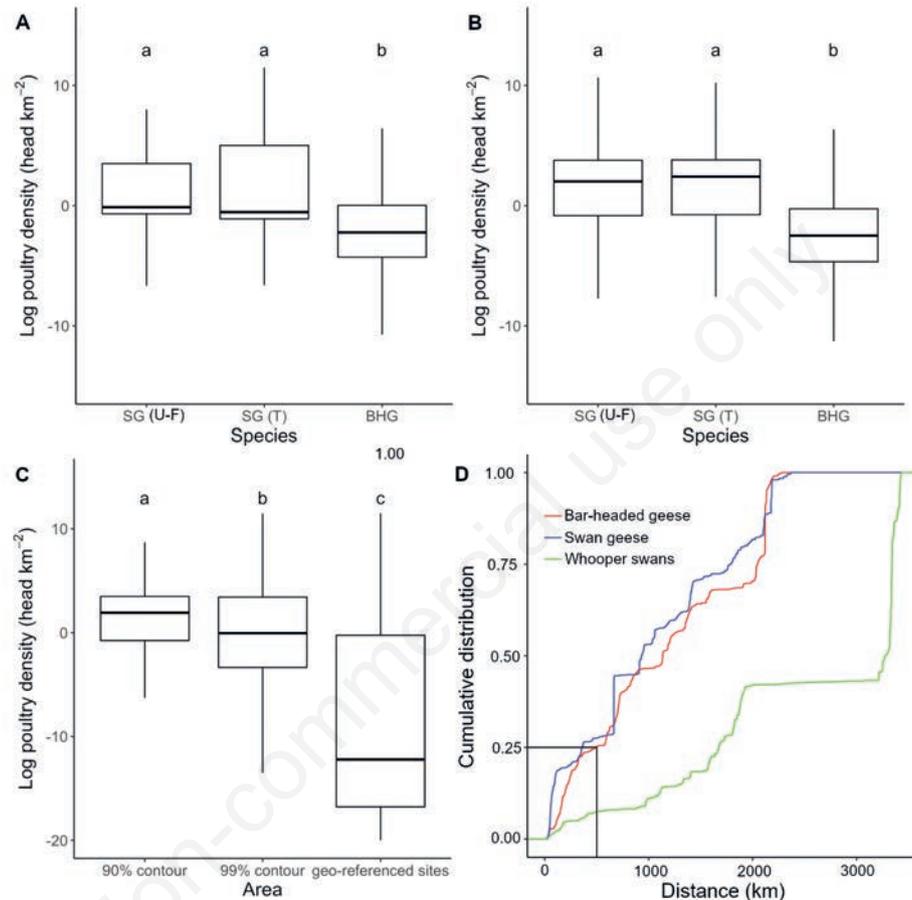


Figure 2. Density differences among domestic ducks in stopover sites for swan geese and bar-headed geese in their migration corridors compared to stopover sites and migration corridors for whooper swans. A) domestic ducks in stopover sites for swan geese (SG) and bar-headed geese (BHG); B) domestic ducks in migration corridors for swan geese and bar-headed geese; C) domestic ducks in stopover sites and migration corridors for Mongolia-South Korea population of whooper swans and geo-referenced sites for Russia-Korea population of whooper swans; D) cumulative density distribution of geographic distances of marked bar-headed geese from 2008 and 2009 combined (red), Swan geese from 2006-2017 combined (blue), whooper swans from 2008-2012 combined (green), respectively, and the total HPAIV outbreaks from 2004-2017. (a), (b) and (c) indicate significantly different groups on the basis of Bonferroni corrected *post hoc* tests. 'U-F' and 'T' in (A) and (B) represent the population marked by USGS/FAO and Tsinghua University, respectively.

Table 2. Summary of outbreaks in different bird populations.

Population	Outbreaks in the study populations	Outbreaks in other species*
Swan goose	0	20
Bar-headed goose	11	48
Whooper swan (Mongolia-S. Korea)	0	67
Whooper swan (Russia-Japan)	37	44

*In wild birds and poultry birds using the study species' migration corridor; the whooper swan populations were included to provide a comparison of one species with two different migration routes.



2017). Migratory individuals have larger immunological organs than resident birds (Møller & Erritzøe, 1998) due to frequent exposure to pathogens during migration (Brown *et al.*, 2008). The whooper swan population that had a higher probability of contact with domestic ducks had no HPAIV outbreak records, whereas the whooper swan population that had a lower probability of contact with domestic ducks was associated with more HPAIV outbreaks (Figure 2). This is consistent with our findings for differences between swan geese and bar-headed geese, as birds with a higher probability of contacting poultry had fewer HPAIV outbreaks (Figure 2A and B; Table 2). Frequent contacts with domestic ducks may increase innate immunity responses in swan geese. We found that the densities of domestic ducks were significantly higher in the East Asian-Australasian Flyway, especially near Poyang Lake where 14 million domestic ducks are produced annually (Cappelle *et al.*, 2014) with the ratio of domestic ducks to wild birds being around 5:1 (Takekawa *et al.*, 2010b). Thus, the HPAIV transmission risk between swan geese and domestic ducks are substantially higher here (Wang *et al.*, 2013; Cappelle *et al.*, 2014). Furthermore, swan goose has a long contact history with domestic ducks in East Asia (Darwin, 1859; Niu, 2016), which might be a selective driver for higher levels of innate immunity (Møller & Erritzøe, 1998). In addition, domestic swan goose is a common poultry species in this region, meaning that viruses circulating in domestic poultry may also be better adapted to this species and thereby counteract any enhanced immunity from increased exposure.

Secondly, although bar-headed geese are well-known victims of HPAIV outbreaks in the wild (Chen *et al.*, 2005; Takekawa *et al.*, 2010b), only 2 of 8 bar-headed geese died in experimental HPAI H5N1 infections (Brown *et al.*, 2008; Nemeth *et al.*, 2013). This mortality rate (25%) is lower compared with other waterfowl species (Brown *et al.*, 2008; Møller & Erritzøe, 1998) indicating that, in non-migration conditions, bar-headed geese may be less vulnerable to HPAI H5N1 infection than other species. However, migrating over the Himalayas and the associated stress of long flight and scaling heights may decrease the immune responses of these geese. Migration is an energetically costly strategy, increasing the metabolic rate 10 times (Battley & Piersma, 2005), a cost that has to be balanced against other expenses, such as immune responses (Altizer *et al.*, 2011; van Dijk & Matson, 2016). For example, migratory barn swallows (*Hirundo rustica*) (Johnson *et al.*, 2014; Møller & Erritzøe, 1998) and thrushes (*Catharus* spp and *Hylocichla mustelina*) (Owen & Moore, 2006) have been found to be immunocompromised compared with non-migratory conspecific ones. The long-distance, high-altitude migration strategy of bar-headed geese is indeed energetically challenging (Hawkes *et al.*, 2011). Some bar-headed goose populations migrate shorter distances between Qinghai Lake and Lhasa, but they need to allocate more energy to withstand the harsh Tibetan climate (Takekawa *et al.*, 2017). Energetically costly migration at high altitudes suppresses immune the immune system (Bishop *et al.*, 2015; van Dijk & Matson, 2016) increasing the vulnerability of bar-headed geese to disease.

In light of these findings, we suggest that more comparative studies should be conducted to examine innate immunological differences among migratory waterfowl species, testing whether contact with domestic ducks stimulate the innate immune reactions against HPAIVs. Furthermore, we suggest physiological studies to investigate whether migration suppresses immune responses. These efforts can be helpful for understanding the HPAIV outbreak

pattern and improving our understanding of pathogen dispersal *via* migratory hosts.

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