

Population dynamics and prevalence of influenza A viruses in Mallard, Mute Swan and other wildfowl

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Introduction

The spread of the Highly Pathogenic Avian Influenza (HPAI) sub-type H5N1 has been an issue of international concern. This spread presents a serious threat to domestic poultry and a potentially serious risk to human health. It is also an issue which could imaginably have consequences for populations of wild birds and other animal species of conservation concern. As aquatic birds, and wildfowl (ducks, swans and geese) in particular, have been known for some time to be the natural reservoir of avian influenza (AI) viruses, potential effects of AI on populations of this avian group are of interest.

Because the dynamics of animal populations are driven by the balance of reproduction and mortality, information on survivorship is vital to understanding these dynamics. In order to assess the risk of AI to populations of wild birds, information on three basic issues is essential: (i) the (range in) mortality rates occurring in the absence of (elevated levels of) AI infection, (ii) the (range in) prevalence of AI viruses in wild bird populations, and (iii) the pathogenicity of AI infections in wild birds, particularly the proportion of infected animals that dies. With this information, the magnitude of potential AI-induced mortality may be compared to mortality rates occurring under 'natural' conditions, allowing an evaluation (e.g., with the use of population models) of possible consequences for population size and persistence of wildfowl populations.

For many avian taxa there is little quantitative information available on survival and its variation in relation to age, gender and other factors. However, some widespread species of wildfowl have been studied extensively, especially Mallard *Anas platyrhynchos*. In North America, annual survival rates of this species have been analysed on various locations over the past decades, mostly in relation to hunting activities and wildlife management. During recent outbreaks of the HPAI H5N1 virus in Eurasia mortality has been observed in Mute Swans *Cygnus olor* and in several other species. Still, many questions about mortality in wild birds due to infection with influenza A viruses are left unanswered. With the increased interest regarding possible threats to human health, a rapidly growing number of studies has recently been devoted to the epidemiology, ecology and evolution of influenza A viruses in their natural hosts. Accordingly, the number of tested wild birds has grown enormously.

In order to achieve a better understanding of wildfowl population dynamics in relation to avian influenza we have performed a literature study on mortality rates and prevalence and pathogenicity of AI viruses in wildfowl under field conditions, focusing on two species: Mallard and Mute Swan. The population dynamics of both species have been relatively well studied, and experiences during HPAI outbreaks in wild wildfowl in Europe in the winter of 2005/06 have indicated that Mute Swans can be rapidly and severely affected compared to other species, making them a potential 'sentinel' species for the occurrence of the virus. Although the focus is on these two species, a brief comparison with other wildfowl taxa is made to put the findings in a wider perspective. This review is divided into three sections, the first dealing with survival rates, the second with prevalence of influenza A viruses in wildfowl and the third with mortality of infected birds and possible impact on a population scale.



Methods

We searched the scientific literature for publications addressing 'mortality', 'survival', 'avian influenza' and similar keywords in ducks and swans, using the electronic databases available in the Web of Science. We augmented this by further searches on the internet. For mortality data, we consulted and assembled primary sources. We focused on estimates of annual survival rates (as opposed to intensive studies on survival during parts of the year) and used mainly studies published after 1970, because the statistical methodology for analyzing ring recoveries and mark-resighting data has developed considerably over the past decades, and the reliability of estimates has increased over time. Concerning prevalence of AI in wild birds, several thorough recent reviews were available and we have relied heavily on these.



Survival of Mallard, Mute Swan and other wildfowl

General

Annual survival probability can be defined as the probability that a bird alive in year i will survive to the banding period in year $i + 1$. Annual mortality is the complement of survival, i.e. mortality = 1 - survival. Survival is usually measured by following marked individuals through time. Individual marks most used in wild birds are numbered metal leg rings that can be read when birds are recaptured or found dead, or coloured leg rings, neck collars or nasal tags that can be read from a distance on live birds. Most survival estimates for ducks are based on analysis of recoveries of dead birds, reported to the ringing offices by the general public or by hunters. Survival studies in geese and swans, particularly the more recent ones, more often use live resightings of colour-marked individuals. A third method is the use of ratio-tags attached to birds, allowing close surveillance of survival (and often also identification of the cause of death), but usually during short time periods only. Radiotelemetry has been extensively used to measure survival of ducks during the breeding season. Obtaining accurate estimates of survival rates of birds thus strongly depends on possibilities for capturing and banding or radio-marking them. Only in some populations (mainly of geese) that can be counted accurately within a restricted (wintering) range and in which the proportion of first-year birds can be reliably assessed by visual observation, estimates of adult survival have been made on the basis of annual changes in total numbers, corrected for the recruitment of young birds.

Survival of wildfowl is subject to considerable variation, since favourable and harsh conditions alternate in both space and time. Survival probability varies considerably not only between avian taxa but also within them. Various studies have shown that juvenile wildfowl typically exhibit low rates of annual survival compared to older individuals (Anderson 1975, Johnson *et al.* 1992, Arnold & Clark 1996). Differences between sexes, regions, seasons and years have been described too, making the interpretation of data, in general, rather complex (*cf.* Gould & Nichols 1998, Giuidice 2003, Lake *et al.* 2006). However, some clear patterns may emerge.

Mallard

The Mallard is one of the best-known species of the family *Anatidae*, which includes swans, geese and ducks. It belongs to the subfamily *Anatinae* and breeds throughout the temperate and subtropical areas of Eurasia and North America, with introduced populations in Australia and New Zealand. The nominate subspecies is found in most of its range, while other subspecies have been described for populations in Greenland, southern USA, Mexico and the Hawaiian Archipelago (Ogilvie & Young 1998). Most northern populations are migratory, wintering at more southern latitudes. It is a medium-sized bird of 50-65 cm, varying in weight between 850-1572 g (males) and 750-1320 g (females) (Cramp & Simmons 1977). Furthermore, it is the ancestor of nearly all domestic duck breeds, except those of Muscovy Duck *Cairina moschata*.

The typical lifespan of Mallard is about 3 years but it has been known to live up to 29 years (www.bto.org, Cramp & Simmons 1977). Numerous studies have looked at annual survival in this species, mainly in North America. In the USA and Canada, widespread hunting of wildfowl is associated with a comprehensive body of research in which population trends and vital rates (reproduction and survival) are monitored and bag limits and other hunting regulations are adjusted based on this research ('adaptive management', Williams & Johnson 1995, Johnson & Williams 1999). This is in stark contrast to the situation in Europe, where some duck species are also hunted in most countries, but quantitative studies on the associated mortality (other than simple bag statistics) have been very scarce, and monitoring of vital rates



is lacking almost completely (Elmberg *et al.* 2006).

Table 1 presents a summary of published annual survival rates of Mallards. Conditions and methodology in these studies vary, but the majority of estimates were derived from analysis of ring recovery data. Different published studies sometimes overlap in the geographical or temporal range of the data analysed, hence data for individual birds may have been included in several estimates, but the means and ranges of the published estimates provide insight in general patterns and the range of variation in survival rates. The majority of data originate from Canada and the USA, but they also include an analysis from New Zealand, as well as a few mainly older studies from Europe.

Estimates of annual survival in Mallards average about 56%, but range between 24% and 71% (Table 1). Several studies have shown that annual survival rates vary between the sexes and between age groups. A general pattern is that juvenile Mallards have lower annual survival rates than adults and

Table 1. Annual survival estimates for Mallards, summarised by sex and age groups. Means, standard deviations and minimum and maximum are based on 49 separate estimates given for age/sex groups for different areas and time periods (listed in Appendix 1).

| Age/Sex group | No. of studies | Mean annual survival | SD | minimum | maximum |
|------------------|----------------|----------------------|------|---------|---------|
| all | 49 | 0.56 | 0.10 | 0.24 | 0.71 |
| juveniles | 18 | 0.51 | 0.12 | 0.24 | 0.71 |
| adults | 21 | 0.58 | 0.08 | 0.36 | 0.68 |
| males | 19 | 0.61 | 0.07 | 0.44 | 0.69 |
| females | 23 | 0.55 | 0.08 | 0.36 | 0.71 |
| adult males | 8 | 0.64 | 0.03 | 0.60 | 0.68 |
| adult females | 10 | 0.55 | 0.05 | 0.47 | 0.61 |
| juvenile males | 7 | 0.54 | 0.07 | 0.44 | 0.62 |
| juvenile females | 8 | 0.54 | 0.12 | 0.36 | 0.71 |

adult females experience lower rates than adult males. The annual survival probabilities of North American Mallards between 1961 and 1970 estimated by Anderson (1975) provide a clear illustration, being 0.50 for juveniles, 0.56 for adult females and 0.63 for adult males. However, age differences in survival in females are often less clear than in males (Table 1).

Explanations for these patterns can be found in age- and gender-specific factors, such as experience and behaviour. Juvenile Mallards experiencing poor conditions for the first time may be more likely to die than adults, and juveniles are also more susceptible to hunting mortality. In adults, breeding effort seems to take a toll especially on females. The (predation) risks associated with incubation and brood rearing are well documented (Cowardin *et al.* 1985, Blohm *et al.* 1987) and lead to an inverse relationship between breeding effort and survival (Dufour & Clark 2002, Devries *et al.* 2003).

The analysis by Dufour & Clark (2002) of survival of yearling (one year old) and adult females in relation to breeding habitat conditions in the Canadian Prairie-Parkland Region support the hypothesis that breeding effort reduces survival. These authors found that yearling females survived at higher annual rate (0.58 ± 0.05) than adult females (0.47 ± 0.03) and that this difference was most pronounced in years of low wetland abundance, when only a small proportion of yearlings attempt to breed. Adult females were more likely to breed also in



years when less breeding habitat was available, and their survival was both lower and less affected by wetland availability. Similar age differences were already reported by Reynolds *et al.* (1995).

Several studies have looked directly into the survival of female Mallards during the breeding season by monitoring radio-marked individuals (e.g. Dwyer & Baldassarre 1993, Losito *et al.* 1995, Devries *et al.* 2003, Hoekman *et al.* 2006). Most of them show strong evidence for reduced mid-seasonal survival of breeding female Mallards and suggest that predation during incubation and brood rearing is the primary source of this mortality. Estimates of adult female mortality over the breeding season are in the range of 12-38% (mean 20-25%), which is a significant proportion of the average total annual mortality of females (*ca.* 45%, Table 1). Brasher *et al.* (2006) found a much lower breeding season mortality in males (1-15%), which take no part in incubation and chick-rearing. Hence, the breeding season is the most risky part of the annual cycle for female Mallards, but not for males.

Survival of Mallards during specific periods outside the breeding season has been less well documented. Berghan & Smith (1993) monitored radio-marked females during three winters in Texas, USA. They estimated a mean survival rate for the 100-day period between 21 November and 1 March of 0.78 ± 0.04 . Individuals in good body condition experienced higher survival than those in poor condition.

Mortality rates may differ between Mallard populations in part because of differences in hunting pressure. A few North American studies have tried to quantify the effect of hunting losses on total annual mortality. Pollock *et al.* (1994) used ring recovery models combined with data on reporting rates and crippling losses (birds shot but not retrieved) from questionnaires among hunters and estimated that of the 38% total annual mortality of Mallards in California in 1980-1983, 16% could be attributed to shooting. Smith & Reynolds (1992) compared mortality rates of Mallards from the prairie regions of Canada and northern USA between periods with liberal (1979-84) and restrictive (1985-88) hunting regulations and found that mortality rates were reduced in the second period in all age-sex classes (by 9-28%).



Mute Swan

The Mute Swan is a well-known monotypic species of the family *Anatidae*, which includes swans, geese and ducks. It belongs to the subfamily *Cygninae* and breeds through the temperate Eurasia, with introduced populations in North America, South Africa, Australia, New Zealand and Japan (Ogilvie & Young 1998). Northerly breeders are migratory, wintering at more southern latitudes, but many populations are resident. It is a large bird of 145-160 cm, varying in weight between 8.1-14.3 kg (males) and 5.5-10.8 kg (females) (Cramp & Simmons 1977).

The typical lifespan of Mute Swan is about 7 years but it has been known to live up to 26 years (www.bto.org). Maturity is delayed and most birds start breeding only at 3-4 years of age, and Mute Swan populations usually include a large pool of subadult and young adult non-breeders (Ebbinge *et al.* 1998, Watola *et al.* 2003). Table 2 presents an overview of published annual survival rates. Survival increases with age. Studies from the USA, where breeding populations have established relatively recently from birds released or escaped from captivity, have tended to find somewhat higher survival rates than studies in western Europe, where the species has bred for a few centuries. In both Europe and North America, survival is negatively affected by severe winter weather, more so in young birds than in older ones (Reese 1980, Ebbinge *et al.* 1998).

Table 2. Estimates of annual survival in Mute Swans by study and age group.

| Region / country | 1 st year | 2 nd year | subadults (3-5 yrs) | adults | Reference |
|------------------------------------|----------------------|----------------------|------------------------|--------|---|
| UK Wiltshire | 0.68 | 0.73 | 0.71 | 0.90 | Watola <i>et al.</i> 2003 |
| UK West Midlands | 0.72 | 0.68 | 0.70 | 0.72 | Coleman <i>et al.</i> 2001 |
| UK | 0.68 | 0.65 | 0.75 | 0.81 | Beer & Ogilvie 1972 |
| UK | 0.58 ¹ | | | 0.80 | Balmer & Peach 1997 |
| UK, Denmark, Netherl. ² | 0.60 | | 0.63 | 0.85 | Bacon & Anderson-Harild 1989 ⁴ |
| UK, Denmark, Netherl. ³ | 0.10 | | 0.40 | 0.70 | Bacon & Anderson-Harild 1989 ⁴ |
| USA Chesapeake Bay | 0.83 | 0.91 | | 0.93 | Reese 1980 |
| USA Michigan | 0.86 ¹ | | | 0.95 | Gelston & Wood 1982 |

¹ Annual survival for 0-3 yr old birds; ² In normal winters; ³ In severe winters; ⁴ augmented with unpublished data from Zwanenwerkgroep Avifauna Groningen, from Ebbinge *et al.* 1998.

Survival and mortality in other wildfowl species

Krementz *et al.* (1997) reviewed the existing literature on survival estimates in wildfowl. Their data, supplemented with a number of subsequently published studies (averaged by species) are shown in figure 1. The major patterns emerging are a clear increase with body mass, and differences in overall survival levels between phylogenetic groups, with geese and seaducks (the two heaviest ducks in Fig. 1) showing relatively high survival rates for their mass. Both Mallard and Mute Swan appear to fit well into this pattern, and show survival rates that are similar to similar-sized species. These patterns partly reflect a life-history continuum (Saether 1987, 1989), with the smaller ducks exhibiting a 'fast' type of population dynamics, with low survival but large clutch size, fast juvenile development and low age at first breeding (1-2 years), and the larger geese and swans exhibiting 'slower' dynamics with smaller clutch size (particularly geese) and delayed maturity (particularly in swans) offset by a higher adult survival rate. These differences may be relevant with respect to the sensitivity of populations to severe mortality events; in ducks these may be more quickly compensated by reproduction than in swans and geese.

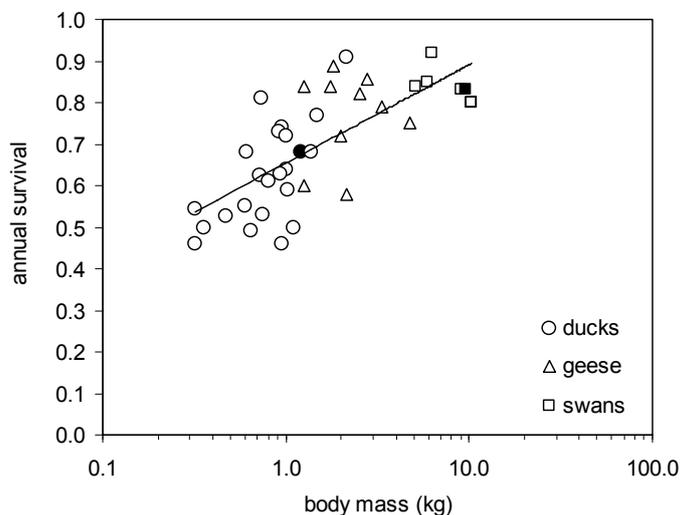


Figure 1. Relationship between average annual (adult) survival rate and body mass in 40 species of swans, geese, and ducks. Black symbols denote values for Mallard (circle) and Mute Swan (square). The regression equation for this relationship is: $Survival = 0.103 \times Mass + 0.655$ ($R^2 = 0.52$).



Prevalence of Influenza A virus in Mallard, Mute Swan and other wildfowl

Influenza A viruses and HPAI outbreaks

Influenza A viruses are classified on the basis of two proteins found on the surface of virus particles, namely the hemagglutinin (HA) and neuraminidase (NA) glycoproteins. They are commonly found in aquatic birds, such as ducks, geese, swans, gulls, terns and waders. In fact, aquatic birds are believed to form the main natural reservoir for influenza A viruses (Fouchier *et al.* 2003, Hanson *et al.* 2003, Wallensten *et al.* 2007). Influenza viruses representing 16 HA and 9 NA antigenic subtypes have been detected in birds throughout the world. Such viruses are better known by their combinations, such as H1N1, H5N1, etc (Munster 2006).

Only influenza viruses of subtypes H5 and H7 are known to become highly pathogenic after introduction in poultry and can cause HPAI outbreaks (also known as 'fowl plague'). The role that wild birds play in the geographic spread of HPAI viruses is still a much debated subject, but it is clear that HPAI outbreaks in poultry find their origin in the low pathogenic influenza A viruses present in wildfowl (*cf* Munster *et al.* 2006). In the past decade, HPAI outbreaks have occurred frequently in various countries around the world, involving viruses of subtypes H5N1, H5N2, H7N1, H7N3, H7N4 and H7N7 (Olsen *et al.* 2006).

Long-term surveillance studies of the prevalence of AI viruses in wild birds have been conducted only in North America (Hanson *et al.* 2003). In the light of possible threats that HPAI viruses pose to human health, the screening of wild birds has recently increased also in Europe and other parts of the world. After all, continuous surveillance studies of wild birds can function as a sentinel system, which can be used to forecast HPAI outbreaks in poultry. Apart from that, it can also offer new information on the ecology and evolution of influenza A viruses in wild birds. A recently described novel influenza A virus hemagglutinin subtype (H16) obtained from Black-headed Gulls *Larus ridibundus* in Sweden illustrates this (*cf* Fouchier *et al.* 2005).

Prevalence of influenza A virus in Mallard, Mute Swan and other wildfowl

Low Pathogenic Avian Influenza (LPAI) viruses have been found in more than 100 bird species of 26 different families. Olsen *et al.* (2006) and Munster *et al.* (2007) presented overviews of the prevalence of influenza A viruses in these taxa. The vast majority of species that have shown high prevalence belong to two groups of birds, namely Anseriformes (particularly ducks, geese and swans) and Charadriiformes (particularly gulls, terns and waders). Their findings with regard to the first group are summarized in table 3. Dabbling ducks of the genus *Anas*, of which Mallard is undoubtedly the best studied species, are infected with influenza A viruses more frequently than other birds. The comparatively low prevalence of diving ducks of the genus *Aythya* can be partly related to behavioral characters; diving ducks forage at deeper depths and more often in large open water systems, including marine habitats. Dabbling ducks shed virus via faeces in the same surface waters where they feed. Swans and geese generally also show a lower prevalence than dabbling ducks. Their different feeding habits and smaller population size may help explain this (Munster *et al.* 2007).



Table 3. Prevalence of influenza A viruses in Anseriformes (after Olsen *et al.* 2006 (worldwide) and Munster *et al.* 2007 (worldwide, but most data from Europe). There is partial data-overlap between studies. The group totals include species not listed separately (usually with small sample sizes).

| Group | Species | Olsen <i>et al.</i> 2006 | | Munster <i>et al.</i> 2007 | |
|-------|---|--------------------------|------------|----------------------------|------------|
| | | N sampled | % positive | N sampled | % positive |
| ducks | | 34.503 | 9.5 | 13.731 | 6.9 |
| | dabbling ducks | 28.955 | 10.1 | 13.279 | 6.1 |
| | diving ducks | 1.011 | 1.6 | 99 | 4.0 |
| | Mallard <i>Anas platyrhynchos</i> | 15.250 | 12.9 | 8.938 | 7.3 |
| | American Black Duck <i>Anas rubripes</i> | 717 | 18.1 | | |
| | Gadwall <i>Anas strepera</i> | 687 | 1.5 | 298 | 2.7 |
| | Northern Pintail <i>Anas acuta</i> | 3.036 | 11.2 | 448 | 2.9 |
| | Northern Shoveler <i>Anas clypeata</i> | 59 | 28.8 | 135 | 3.7 |
| | Eurasian Wigeon <i>Anas penelope</i> | 1.023 | 0.8 | 2.538 | 3.0 |
| | Blue-winged Teal <i>Anas discors</i> | 1.914 | 11.5 | | |
| | Common Teal <i>Anas crecca</i> | 1.314 | 4.0 | 940 | 6.4 |
| | Green-winged Teal <i>Anas carolinensis</i> | 707 | 4.0 | | |
| | Spot-billed Duck <i>Anas poecilorhyncha</i> | 574 | 3.7 | | |
| | Wood Duck <i>Aix sponsa</i> | 926 | 2.2 | | |
| | Tufted Duck <i>Aythya fuligula</i> | 266 | 1.1 | 62 | 3.2 |
| | Common Eider <i>Somateria mollissima</i> | | | 37 | 5.4 |
| | Common Shelduck <i>Tadorna tadorna</i> | 881 | 6.5 | 335 | 0.6 |
| geese | | 4.806 | 1.0 | 6.428 | 1.8 |
| | Canada Goose <i>Branta canadensis</i> | 2.273 | 0.8 | 376 | 0.0 |
| | Barnacle Goose <i>Branta leucopsis</i> | | | 1.139 | 0.7 |
| | Brent Goose <i>Branta bernicla</i> | | | 413 | 1.0 |
| | Greylag Goose <i>Anser anser</i> | 977 | 1.1 | 455 | 2.4 |
| | Bean Goose <i>Anser fabalis</i> | | | 315 | 0.6 |
| | Pink-footed Goose <i>Anser brachyrhynchus</i> | | | 285 | 2.1 |
| | White-fronted Goose <i>Anser albifrons</i> | 596 | 2.2 | 3.821 | 2.1 |
| | Egyptian Goose <i>Alopochen aegyptiacus</i> | | | 100 | 0.0 |
| swans | | 5.009 | 1.9 | 220 | 2.0 |
| | Tundra Swan <i>Cygnus columbianus</i> | 2.137 | 2.8 | 153 | 3.0 |
| | Mute Swan <i>Cygnus olor</i> | 1.597 | 1.3 | 47 | 2.1 |
| | Whooper Swan <i>Cygnus cygnus</i> | 930 | 1.5 | 26 | 0.0 |

Various studies have revealed high LPAI virus prevalence primarily in juvenile ducks (Alfonso *et al.* 1995, Olsen *et al.* 2006, Wallensten *et al.* 2006), suggesting that these birds' immunological naivety plays an important role. For instance, Munster *et al.* 2007 reported AI prevalence of 6.8% in juvenile against 2.8% in adult Eurasian Wigeon *Anas penelope* and Mallards. Young birds can thus be seen as the 'high risk group' in wildfowl, as was already reported by e.g. Hinshaw *et al.* (1980) and Slemons *et al.* (1991). A significant relationship between gender and LPAI virus prevalence has not been found (Alfonso *et al.* 1995, Munster *et al.* 2007).

In the Northern Hemisphere the highest prevalences are detected in early autumn, at the start of the migrating season of many species. In this period LPAI virus prevalence in ducks of up to 60% has been reported in North America (Olsen *et al.* 2006). During winter the prevalence typically falls to a much lower level (0.4-2%) and remains low (ca. 0.25%) during the return migration in spring. In Europe, a similar pattern has been observed, although virus detection during spring can be significantly higher (up to 6.5%) (Olsen *et al.* 2006). Locations where large numbers of birds congregate, such as breeding colonies and migration stopover sites,



seemingly create good opportunities for virus spread. Several surveillance studies have observed higher prevalence in northern latitudes than at more southern sites (e.g. 15-20% in Mallards in Sweden vs. 5-7% in The Netherlands in August-November of the same years), suggesting that high virus prevalence early in the autumn gradually declines as the migration proceeds (Munster *et al.* 2007). Little is known about the prevalence in the Southern Hemisphere, or potential transmission between the two hemispheres.

Monitoring in Mallards the Netherlands in 1999-2005 revealed peak prevalence in September-October in most years, but with one exception (January). Peak prevalences varied between years from 0.9% to 20.8%. Similar fluctuations in annual peak prevalence were observed in Eurasian Wigeon (0.8-20%) and Common Teal *Anas crecca* (4-30%) (Munster *et al.* 2007).

Although almost all known HA and NA subtypes circulate in wild ducks in North America and northern Europe, H3, H4 and H6 were isolated most frequently. Subtype H13, as well as the recently described H16 seem to occur primarily in gulls. There is reason to believe that the prevalence of different subtypes varies over time, place and species, possibly following cyclic patterns (*cf* Olsen *et al.* 2006).

Mortality rates of infected wildfowl

LPAI virus infections usually cause no clinical signs in dabbling ducks and other wildfowl, which is compatible with the notion that these species form the natural reservoir of LPAI viruses (Olsen *et al.* 2006). However, the lack of readily observable clinical symptoms does not mean that the virus has no detrimental effects on the birds' fitness, even if only through a reallocation of resources to boost the immune system. Three Bewick's Swans *Cygnus bewickii* infected with LPAI exhibited significantly lower rates of food ingestion and premigratory fuelling, departed almost a month later, and made shorter migratory flights before refuelling than non-infected conspecifics marked on the same date (Van Gils *et al.* 2007). It is likely that either reproduction or longer-term survival of the infected individuals will have been impaired by these effects. Although it could not be fully established that the AI infection of the birds was the cause and not a consequence of their poor performance, this study points to the possibility that LPAI infection entails serious fitness costs to wildfowl that are nevertheless difficult to observe.

Since the HPAI H5N1 virus occurred in poultry farms in Hong Kong in 1997 and resulted in the first reported case of human influenza and fatality, the virus has been detected in both poultry and wild birds several times. In contrast to LPAI, infections with HPAI have caused mortality in wild birds, sometimes on a massive scale. In 2005 the virus was isolated at Quinhai Lake, China, where ca. 6000 wild birds were lethally affected (Zhou *et al.* 2006). Among them were ca. 3000 Bar-headed Geese *Anser indicus*, a species breeding exclusively in central-Asia. It was estimated that the species suffered a 10% decline of the global population from this one event (Olsen *et al.* 2006, Zhou *et al.* 2006). In Europe mortality has been reported in a number of bird species, particularly in Mute Swan and Whooper Swan *Cygnus cygnus* (e.g. Nagy *et al.* 2007). In all, the virus strain that originated in South-East Asia has caused mortality in more than 60 species of birds (Olsen *et al.* 2006). Still, much remains uncertain about mortality rates of HPAI infected birds. Mass mortality has not been the rule among concentrations of wild aquatic birds where H5N1 has been known to be present, and several clinical trials have shown that (domestic) ducks can survive infection with the virus without even showing overt clinical signs, although geese seemed to be more readily affected in similar trials (e.g. Perkins & Swayne 2002, Chen *et al.* 2005). Laudert *et al.* 1993 found only minor or no effects of H5N1 infection on egg production and growth of young in domestic ducks.



Potential effects of avian influenza viruses on wildfowl populations

We set out this review by noting that assessing the potential effects of AI viruses on natural wildfowl populations requires information on three key issues: natural mortality rates, prevalence of AI in natural populations, and pathogenic effects of AI on infected wild birds. This review has shown that there is a reasonably good body of information on (variation in) mortality rates in wildfowl. Our knowledge of patterns in AI prevalence in wild birds is less comprehensive, but rapidly increasing now that extensive surveillance programs have been set up in different parts of the world. On the other hand, scientists have barely scratched the surface of the third issue. Quantitative studies of pathogenic and fitness effects of AI infections in wild birds are still virtually lacking, and most clinical tests have been conducted in laboratory settings and on domestic wildfowl strains. Moreover, the existing results range from no observable clinical effects to mass mortality. Clearly, this is currently the major gap in our knowledge. Until more data are available and a better understanding has been gained of the factors influencing the effect of AI infections on individual fitness, evaluations of the potential impact of AI on aquatic bird populations will remain conjectural.

However, a single observation may be made even in the absence of much information. The mortality event in Bar-headed Geese at Qinghai Lake has shown that 'worst case scenarios' may come true in practice. It seems likely that the risk of population extinction will be smaller in wildfowl taxa with large, widespread and migratory populations than in species or subspecies with a small population exhibiting local movements within a restricted range. In the former group, total population size is less affected by a mass mortality event, and population recovery may be enhanced by immigration of birds from elsewhere in the species' range, in addition to local breeding productivity. Taxa that are most vulnerable to other types of demographic perturbation may thus also be most vulnerable to AI outbreaks. The Bar-headed Goose itself provides a point in case. European examples of such vulnerable taxa are White-headed Duck *Oxyura leucocephala* and Marbled Duck *Marmaronetta angustirostris*, and among the more migratory species, Lesser White-fronted Goose *Anser erythropus* and Red-breasted Goose *Branta ruficollis*. In surveillance programs special attention could be given to the wetlands areas where these species occur, and clinical studies on effects on AI infection should be made also on these species, e.g. making use of birds from captive wildfowl collections.



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