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Ecological Aspects of Influenza A Virus Circulation in Wild Birds of the Western Palearctic

M. Delogu[1]*, M.A. De Marco[2], I. Donatelli[3], L. Campitelli[3] and E. Catelli[1]
[1] *Dipartimento di Sanità Pubblica Veterinaria e Patologia Animale, Facoltà di Medicina Veterinaria, Università degli Studi di Bologna, Ozzano Emilia (BO);* [2] *Istituto Nazionale per la Fauna Selvatica, Ozzano Emilia (BO);* [3] *Laboratory of Virology, Istituto Superiore di Sanità, Rome, Italy.*
* *Correspondence: Dipartimento di Sanità Pubblica Veterinaria e Patologia Animale, Facoltà di Medicina Veterinaria, Università degli Studi di Bologna, 50 via Tolara di Sopra, 40064 Ozzano Emilia (BO), Italy*
E-mail: delogu@vet.unibo.it

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INTRODUCTION

The role of wild animals in the ecology of influenza is considered to be very important. Many researchers consider the natural reservoirs of the influenza A virus to be wild birds, principally those belonging to the Order Anseriformes. Many influenza viruses, showing all the possible haemagglutinin (HA) and neuraminidase (NA) antigenic combinations, have been isolated from birds belonging to 88 species, 22 families and 12 orders all belonging to the Class Aves: these various free-living species can assume different epidemiological roles in the natural influenza cycle (Stallknecht and Shane, 1988). Influenza A viruses have also been isolated, although infrequently, from wild mammals such as Mustelidae (*Mustela* spp.) and marine mammals (Pinnipeda, Cetacea) (Webster *et al*., 1992).

When influenza epidemics occur in poultry, wild birds are immediately blamed and systematic attempts to isolate viruses from wild birds are carried out to obtain an epidemiological proof (De Marco, 1998). In fact, the ecology of influenza A viruses is always related to the biological characteristics of the bird species implicated as reservoirs or, eventually, epiphenomena. The ecology of influenza viruses is a very dynamic system in which certain structural constants (reservoir migrations) and other important environmental variables coexist within zoogeographic regions. This system influences both the biology of reservoirs and that of epiphenomena, and in turn their interactions with the virus.

The Western Palearctic is a zoogeographic region that includes Europe, the part of Asia to East Himalaya, a part of Arabia, and the part of Africa to the north of the Tropic of Cancer. This region, together with the Nearctic Region, makes up the

largest zoogeographic region of the western hemisphere, known as the Holoarctic Region. Italy is situated in the central-south-western area of the Palearctic Region and represents an ideal geographic bridge between the northern limits (tundra, northern Europe) and the southern limits (northern Saharan Africa) of the Western Palearctic.

The Italian avifauna include over 400 species classified as biogeographic types. The typologies are as follows: 104 Palearctic; 42 Arctic; 42 Holoarctic; 29 Mediterranean, 28 European; 24 European-Turkestanic; 24 Siberian; 18 Old World; 16 Turkestanic-Mediterranean; 14 Indo-African; 14 Cosmopolitan; 14 Turkestanic; 9 Sarmatic; 9 Paleomontane; 7 Paleoxeric; 6 Siberian-Canadian; 5 North Atlantic; 5 Ethiopic; 4 Paleoxero-Montane; 3 Nearctic; 3 Mongolian-Tibetan; 1 Antarctic; 1 Chinese-Manchurian; and 5 of unknown type (Chelini, 1984). From these data we can deduce that the Italian avifauna is most similar to that of North and Central Europe. As can be seen in the above classification, 25% of the Italian avifauna belong to the Palearctic type while only 7% belong to the Mediterranean type. It is clear that the Italian avifauna is more similar to the Central European types than to the Mediterranean types (Chelini, 1984).

RESERVOIR DISTRIBUTION AND MOVEMENTS

Birds belonging to the Sub-Family Anatinae are the major reservoir of the influenza viruses. The following duck species are present in the Palearctic Region, though their distribution is holoarctic: shelduck (*Tadorna tadorna*), wigeon (*Anas penelope*), gadwall (*Anas strepera*), teal (*Anas crecca*), pintail (*Anas acuta*), eider (*Somateria mollissima*), king eider (*Somateria spectabilis*), harlequin (*Histrionicus histrionicus*), long-tailed duck *(Clangula hyemalis*), common scoter (*Melanitta nigra*), velvet scoter (*Melanitta fusca*), mallard (*Anas platyrhynchos*) and red-breasted merganser (*Mergus serrator*). In the Holoarctic and Oriental regions we can find teal, mallard, pintail, tuffed duck (*Aythya marila*) and goosander (*Mergus merganser*). However, the white-headed duck (*Oxyura leucocephala*) and marbled teal (*Marmaronetta angustirostris*) are found only in the Palearctic region, while the American wigeon (*Anas americana*) and blue-winged teal (*Anas discors)* are found only in the Nearctic Region. The ruddy shelduck (*Tadorna ferruginea*), mandarin duck (*Aix galericulata*), Baikal teal (*Anas formosa*) and redcrested pochard (*Netta rufina*) inhabit the Palearctic and Oriental Regions, while the mallard is the only species to be found in the Holoarctic, Oriental and Australian Regions. The garganey (*Anas querquedula*), pochard (*Aythya ferina*), tufted duck (*Aythya fuligula*), and ferruginous duck (*Aythya nyroca*), can be found in the Palearctic, Ethiopic and Oriental Regions, while the shoveler (*Anas clypeata*) is found in the Ethiopic, Oriental and Holoarctic Regions (Chelini, 1984; Scott and Rose, 1996).

It therefore appears obvious that each species can frequent different zoogeographic areas, but for many the presence in Palearctic Region is a constant. The reasons for

this distribution are given by both the habitat and the distribution of the reproductive (north) and wintering (south) zones. Wild ducks migrate to satisfy several biological needs vital to their survival; these factors vary from species to species, and within the species from population to population. In order to reach the various zones involved in their life cycle, the birds undertake seasonal migration. This migration takes them south in late summer and autumn in the quest for a mild climate, and north to reproductive areas at the end of winter–beginning of spring. During the migration south, the adult birds are accompanied by young birds born during the reproductive season, while, upon return north the entire bird population is potentially reproductive (Scott and Rose, 1996).

Since the cyclic nature of the influenza infection is conditioned by the existence of young birds, this migrational behaviour is of great importance. Furthermore, the migration towards the south is much slower than that north and the birds make numerous stops along the way. The Palearctic Anatidae populations have three different behavioural characteristics: (a) the sedentary species (e.g. ruddy shelduck, white-headed duck and marbled duck) remain for their entire life in the same geographic region); (b) the completely migratory species (smew (*Mergus albellus*), garganey), make a complete migrations between north and south; (c) the partially migratory species (e.g. mallard) constitute the major part of the Anatidae. In the species belonging to the last group, only a part of the population migrate (Chelini, 1984).

The various flyways used by waterfowl to cross the Western Palearctic in order to migrate south are: (1) from Sweden, across France and Gibraltar to Africa; (2) from Finland, across Holland, north-western Italy and Sardinia to Africa; (3) from central Europe across the Balkans, south Italy and Sicily to North Africa. Other routes, which cover more easterly zones are (4) from central Europe, over the Balkans and Greece to North Africa; (5) from Central Europe across the Black Sea and Turkey to East Africa (Scott and Rose, 1996). Except for garganeys, which winter in western Africa and migrate over the Sahara desert, all other species winter in the Mediterranean wetlands. The wintering areas of most of the waterfowl that migrate in spring and autumn are found in Italy; these same areas are also the breeding sites for some partially migratory species such as mallards. Waterfowl migrations are studied by catching and ringing wild birds and by verifying the sites of recapture. From the data obtained, it is evident that the duck populations wintering in Italy come from north-western Europe (Chelini, 1984; Scott and Rose, 1996).

According to the annual winter census, the total Palearctic waterfowl population fluctuates between 13 and 15 million birds. The most prevalent species of dabbling and diving ducks are: the mallard with five million birds (76 000/115 000 in Italy) and the teal with 2.5 million birds (1 million in the Mediterranean Basin and 51 000/67 000 in Italy). The other species include the wigeon with 1.5 million birds (1 million in the Mediterranean Basin and 71 000–84 000 in Italy); the pintail with 1.3 million birds (about 200 000 in the Mediterranean Region and 6000 in Italy); the shoveler with 1 million birds (10% wintering in the Mediterranean Region and 20 000 in Italy); the gadwall with 5800 birds wintering in Italy; the pochard with 750 000 birds in the

Mediterranean region (about 37 000–43 000 in Italy); and the tufted duck with 6000–8500 birds in Italy (Serra *et al*., 1997; Rose and Scott, 1997; Chelini, 1984; Baccetti *et al*., 2002).

Numerous and varied wintering areas can be found in Italy, representing the various ecological habitats of each species. The diving ducks usually winter in the deep water of the most important Italian lakes and ponds; while dabbling ducks are mainly concentrated in marshes. A great number of different species of waterfowl crowd the highly productive wintering areas, and these areas are shared for a while with many other heterogeneous sedentary or migratory bird species. Thus, homospecific and heterospecific aggregations are formed and are favoured by feed availability and the absence of hunting. This is a favourable situation for the transmission of influenza viruses both between allopatric homospecific populations, and between heterospecific groups (De Marco *et al*., 1999, 2000). During this aggregation, which takes place in autumn and winter, the high population density may allow virus transmission during this period characterized by a low prevalence of influenza infection.

VIRUS SURVIVAL AND HOST/VIRUS INTERACTION

The pH, salinity and temperature of the water may facilitate survival of the virus (Stallknecht *et al*., 1990a, 1990b). By drinking water or filtering it in the quest for food, birds may aquire the virus. The depth and turnover of the water are the main factors that influence the ecological interaction between host and virus. The virus can spread easily in the small highly frequented areas where direct bird-to-bird contact is facilitated by the high population density. Interactions can also be enhanced during the winter season by particularly adverse climatic conditions (ice). The water should be considered as a means of virus preservation as well as of virus transmission, allowing the spread of infection without direct contact between birds. Numerous bird species drink the same water; thus, species that are normally separated because of ethological and ecological limits come into contact when they drink the same water and the virus can circulate freely both in reservoirs and in epiphenomena. The latter are hosts that are generally able to harbour the virus for a limited period but are not able to maintain the disease in the wild.

The influenza virus is characterized by a moderate host-specificity and this provides many epidemiological possibilities: the virus can be transmitted by water to a wide range of birds and mammals. The infection may or may not cause disease. Therefore, most of the more than 400 bird species that constitute the Italian avifauna (Chelini, 1984) could potentially assume the role of an epiphenomenon. Among the epiphemomena, some wild mammals such as Mustelidae and marine mammals, may also be included. The large numbers of bird species found in the Western Palearctic region allow the avian epiphenomena to carry the influenza virus to disparate environments, including urbanized areas, where intensive rearing farms are often located. For this

reason Passeriformes, wild Galliformes and, to a lesser extent, Columbiformes can represent an ecological interface between reservoir species and susceptible domestic birds. If biosecurity measures are not correctly applied, the above-mentioned phenomena can provide the main means for spread of the virus from the reservoirs to domestic poultry.

CONCLUSIONS

The correct interpretation of influenza virus ecology is often difficult because epidemiological research is carried out to explain recent or current disease outbreaks (Wobeser, 1994). Sampling of epiphenomena is often carried out and the role of reservoir is erroneously attributed to these birds. It is often thought that the source of infection for domestic birds is represented only by wild birds. Ducks are the natural hosts of influenza viruses; however, the disease can enter domestic flocks, which can maintain the diverse influenza gene pool (Guan *et al*., 2002). Moreover, a distinction between wild free-living species and the same species kept in captivity is not always made, thus complicating any epidemiological interpretation.

Over the course of evolution, influenza viruses have acquired a versatile ability to interact with hosts and the ability to mutate, thus eluding the host immune defences. The virus has also acquired advantages from the environment: (a) the influenza virus utilizes water for survival and to spread, and (b) the influenza virus is co-evolved in a reservoir (ducks) strictly tied to the water (Horimoto and Kawaoka, 2001). The water in turn is able to influence the movements, the social behaviour and the migration of many waterfowl species. It is of great importance to know the ecological strategy of the influenza virus in order to understand this disease and to control outbreaks when they occur.

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