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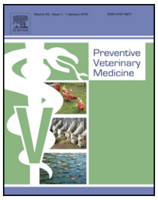

Bridge hosts for avian influenza viruses at the wildlife/domestic interface: An eco-epidemiological framework implemented in southern Africa

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ABSTRACT

Wild terrestrial birds can act as potential local spreaders or bridge hosts for avian influenza viruses (AIVs) between waterfowl (the maintenance hosts of AIVs) and domestic avian populations in which AIVs may cause disease. Few studies have investigated this hypothesis, although it is an important knowledge gap in our understanding of AIV spread within socio-ecosystems. We designed a simple and reproducible approach in an agro-ecosystem in Zimbabwe based on: (1) bird counts at key target sites (i.e., wetlands, villages, intensive poultry production buildings and ostrich farms) to identify which wild birds species co-occur in these different sites and seasons when the risk of AIV transmission through these potential bridge hosts is maximal and (2) targeted sampling and testing for AIV infection in the identified potential bridge hosts. We found that 12 wild bird species represented the vast majority (79%) of co-occurrences in the different sites, whereas 230 bird species were recorded in this ecosystem. Specifically, three species – barn swallow, *Hirundo rustica*, red-billed quelea, *Quelea quelea* and cattle egret, *Bubulcus ibis* – represented the main potential bridge host species (65% of co-occurrences). In two out of these three species (i.e., barn swallow and red-billed quelea), we detected AIV infections, confirming that they can play a bridge function between waterfowl and domestic species in the ecosystem. Our approach can be easily implemented in other ecosystems to identify potential bridge hosts, and our results have implications in terms of surveillance, risk management and control of AIV spread in socio-ecosystems.

1. Introduction

Anseriformes and Charadriiformes are known to maintain low pathogenic avian influenza virus (LPAI) strains, whereas the role of other wild bird species is unclear (Olsen et al., 2006). Although the pathogenic effect of AIV infections on migrating birds is still debatable (Arsnoe et al., 2011), the study of individual bird movements or waves of

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migrating populations in relation to the epidemiology of AIVs in wild birds (Gaidet et al., 2010) indicates that these hosts play a role in the medium- and large-scale spread of LPAI and possibly (highly pathogenic) HPAI (Wang et al., 2008; Reperant et al., 2010). In addition, phylogenetic analyses of LPAI indicated intercontinental movements of strains across waterfowl populations (Koehler et al., 2008). Therefore, understanding the role of wild birds in AIV epidemiology is of paramount importance to understand the spread and emergence of AIV strains between wild and domestic avian populations (including the emergence of HPAI) (Caron et al., 2009).

At finer spatial scales, wild ducks and shorebirds (the main AIV hosts) are rarely in contact with domestic birds (including free-ranging poultry) due to their distinct ecological requirements. The potential epidemiological role of terrestrial birds that share the habitat of waterbirds and visit poultry farms for opportunistic foraging has been proposed as a source of virus transmission between waterfowl and poultry populations (Burns et al., 2012) but little investigated so far (Veen et al., 2007). Risk-based approaches for the local spread of HPAI have identified wild birds as a risk factor for HPAI transmission (Tiensin et al., 2009). More recently, isolation in a tree sparrow (*Passer montanus*) of the newly emerged H7N9 virus in China where it has caused severe human disease, and the evidence of replication of this H7N9 virus in several terrestrial birds, has raised concerns about the potential role of some passerines in the transmission of AIVs with a pandemic potential (Jones et al., 2014; Zhao et al., 2014). Investigating this role is important to better protect poultry populations worldwide as they represent an increasing source of protein for human populations.

In most agro-ecosystems where domestic avian populations are exploited, hundreds of wild bird species cohabit and interact through direct contacts or indirectly by sharing habitat and resources, offering a complex multi-host system for the transmission of AIVs (Caron et al., 2012). In order to identify which wild bird species can spread AIVs between waterfowl and domestic populations in a specific ecosystem, a framework is therefore necessary to identify which species amongst the avian diversity can act as bridge hosts. The requirements to qualify as a bridge host concern the physiology and the ecology of the species' population. First, it links with the capacity for the species to get infected, to replicate and to excrete AIVs, later called the host competence for AIVs. Little is known about the host competence of most wild bird species to AIVs. Specific experimental infection trials have evaluated the competence of only a few species (e.g., Fujimoto et al., 2010), and opportunistic field sampling targeting waterfowl species has provided some additional data, although usually with small sample size (e.g., Caron et al., 2012). Overall, information on host competence is available for a maximum of a few hundreds of species whereas about tens of thousands of bird species occur worldwide. However, based on the available information, most avian orders seem to be susceptible to AIVs, which needs to be confirmed by further experimental studies (Olsen et al., 2006).

The second requirement is that the potential bridge host is in contact with the maintenance population, that is, the waterfowl community, and the target population that one wants to protect, that is, the domestic population (Haydon et al., 2002). By contact, we mean the rate of infectious contacts that lead to pathogen transmission. This parameter is important for epidemiological models but has rarely been investigated empirically and is usually estimated through the contact rate between hosts, a proxy that often overstates the infectious contact parameter, as most contacts do not result in transmission (Richomme et al., 2006). However, the observation of an infectious contact is almost impossible in situ and contacts between hosts remain the best proxy available. At a local scale, an infected bird species undertaking local movements (from a few hundred metres to a few kilometres) while being able to excrete AIVs for a few days can potentially spread AIVs between avian populations. Under these circumstances (i.e., a lack of information on host competence for AIVs and little constraint for virus local spread), the range of eligible bridge hosts is wide.

We developed an eco-epidemiological framework to identify bridge hosts in an agro-ecosystem. We focussed our study on the risk of AIV spread by direct or indirect contact between wild and domestic birds, although we acknowledge the fact that other transmission pathways could be eligible (e.g., poultry trade or human vector). First, we used bird counts to identify wild bird species potentially playing a bridge role in the ecosystem, allowing us to quantify the relative proportion of potential contacts between maintenance, bridge and target hosts and reducing the multi-host complexity by ranking species the most at risk of playing a bridge role. Then, we conducted targeted sampling on the species identified to investigate their exposure to AIVs when present in the ecosystem. Therefore, instead of sampling 'blindly' within the wild bird community, this prioritisation process can help guide AIV surveillance efforts towards the most likely bridge hosts.

2. Material and methods

The epidemiological functions under study are identical to those described in Caron et al. (2012): (1) the 'reservoirs' or 'maintenance hosts' of AIVs are Anseriformes and Charadriiformes, as generally accepted for AIV epidemiology (Olsen et al., 2006); (2) the 'target species' according to Haydon (Haydon et al., 2002) are the host population to be protected from AIV infection; and (3) the 'bridge host' has been defined as a species, non-maintenance for AIVs as defined in (1), competent for AIV and with the potential to spread the pathogen from an infected population to a naive one. A compartment is defined here as "a set of avian populations under similar environmental conditions" (Caron et al., 2009) such as 'waterfowl', 'intensive poultry production farm', 'extensive ostrich farms' or 'backyard poultry'.

2.1. Study site

Lakes Chivero and Manyame in the Manyame river catchment in Zimbabwe are two artificial dams built in the 1950s (respective centroid Global Positioning System (GPS) coordinates for both lakes: 30°33′57″E, 17°49′11″S;