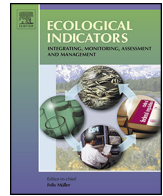




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Bird migration and avian influenza: A comparison of hydrogen stable isotopes and satellite tracking methods



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ABSTRACT

Satellite-based tracking of migratory waterfowl is an important tool for understanding the potential role of wild birds in the long-distance transmission of highly pathogenic avian influenza. However, employing this technique on a continental scale is prohibitively expensive. This study explores the utility of stable isotope ratios in feathers in examining both the distances traveled by migratory birds and variation in migration behavior. We compared the satellite-derived movement data of 22 ducks from 8 species captured at wintering areas in Bangladesh, Turkey, and Hong Kong with deuterium ratios (δD) in the feathers of these and other individuals captured at the same locations. We derived likely molting locations from the satellite tracking data and generated expected isotope ratios based on an interpolated map of δD in rainwater. Although δD was correlated with the distance between wintering and molting locations, surprisingly, measured δD values were not correlated with either expected values or latitudes of molting sites. However, population-level parameters derived from the satellite-tracking data, such as mean distance between wintering and molting locations and variation in migration distance, were reflected by means and variation of the stable isotope values. Our findings call into question the relevance of the rainfall isotope map for Asia for linking feather isotopes to molting locations, and underscore the need for extensive ground truthing in the form of feather-based isoscapes. Nevertheless, stable isotopes from

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feathers could inform disease models by characterizing the degree to which regional breeding populations interact at common wintering locations. Feather isotopes also could aid in surveying wintering locations to determine where high-resolution tracking techniques (e.g. satellite tracking) could most effectively be employed. Moreover, intrinsic markers such as stable isotopes offer the only means of inferring movement information from birds that have died as a result of infection. In the absence of feather based-isoscapes, we recommend a combination of isotope analysis and satellite-tracking as the best means of generating aggregate movement data for informing disease models.

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1. Introduction

The importance of migratory wild birds in the spread of H5N1 highly pathogenic avian influenza (HPAI) is a much-debated topic (Newman et al., 2012; Takekawa et al., 2010b). In areas commonly affected by HPAI, poultry trade is regarded as the primary cause for the persistence and spread of HPAI (Gauthier-Clerc et al., 2007), and long-distance transportation of poultry products along with unregulated practices at poultry markets have been linked to outbreaks in many parts of Asia (Amonsin et al., 2008; Liu et al., 2003; Shortridge et al., 1998; Wang et al., 2006; Yu et al., 2007). Waterbirds (i.e., Anatidae and Charadriidae) have been identified as primary reservoirs for low pathogenic influenza viruses (Stallknecht and Shane, 1988), but with our limited knowledge about the distances infected birds migrate and connectivity among populations, the importance of HPAI transmission by wild birds remains an open question (Gaidet et al., 2010; Takekawa et al., 2010b; van Gils et al., 2007; Weber and Stilianakis, 2007).

The potential of wild birds to spread HPAI is evident in the 2005 outbreak at Qinghai Lake in China that killed more than 6000 wild waterfowl. Poultry farming in this part of the Tibetan Plateau is rare which implies that migratory waterfowl were the likely source of the disease. Subsequent spread of HPAI into Russia, Western Europe, the Middle East, and Northern Africa, provides further evidence of transmission by wild birds (Gilbert et al., 2006b; Normile, 2005, 2006; Prosser et al., 2009), as do genetic similarities among the viruses from these disparate geographic areas (Prosser et al., 2011). In particular, related strains of HPAI along the eastern portion of the Central Asian Flyway provide what is perhaps the strongest evidence of wild bird involvement in HPAI transmission (Newman et al., 2012).

Areas where wild and domestic birds often come into contact have proven particularly prone to HPAI outbreaks, especially regions that feature extensive free-range duck production (Alexander and Brown, 2009; Gilbert et al., 2007; Hulse-Post et al., 2005). Within Thailand, hot spots for H5N1 HPAI outbreaks correspond closely with the density of free-ranging ducks, which serve as a disease reservoir and also often forage next to wild waterfowl known to carry the virus asymptotically (Gilbert et al., 2006a, 2008; Songserm et al., 2006).

Although migration corridors and HPAI outbreaks may not be temporally correlated in some cases (Takekawa et al., 2010a), the potential for transmission (see Gaidet et al., 2010) and gaps in our knowledge about global migration routes warrant further investigation into regional connectivity. Considerable effort has been devoted to tracking waterfowl in areas affected by HPAI (e.g., Batbayar et al., 2011; Iverson et al., 2011; Newman et al., 2009; Prosser et al., 2011; Takekawa et al., 2010a). Although these efforts have generated significant insights into migration routes and the role of wild birds in HPAI transmission, they are limited in extent due to the expense associated with satellite tracking technology. The cost of a single satellite tracking device may exceed \$4000 (USD) including hardware and data acquisition charges. In addition, satellite tags may stop transmitting within a few weeks of deployment, thus failing to convey tracking data for a full annual cycle (see methods and Cappelle et al., 2011).

Stable isotope ratios in feathers offer an alternative means of evaluating population connectivity in migratory birds (Hobson, 2005; Hobson et al., 2009b). Stable isotope ratios of hydrogen vary predictably across the landscape, and the keratin generated during feather growth typically reflects stable isotope ratios in the local environment (Hobson and Wassenaar, 2008). By analyzing feathers collected at a waterfowl wintering location, we can infer the geographic region where breeding and feather molt occurred during the previous summer and fall. The resolution of this tracking technique is low and the inference from a single sample is often quite poor (Kelly et al., 2008; Wunder et al., 2005). However, a modest sample of feathers from 20 to 50 individuals can provide useful information about distances traveled as well as variability in migratory behavior. Although detailed migration routes are not obtainable from isotope data, this method is relatively inexpensive (most facilities charge less than \$50 USD per sample), and it can be used for birds of any size. In contrast, the smallest satellite transmitters currently available can only be used on birds that weigh over 100 g (Bridge et al., 2011). Lastly, of particular importance for disease studies is that feather-isotopes can be quantified from samples collected from birds that have died as a result of an outbreak, allowing for potential inference of the provenance of the disease.

It should be noted that the meaning of “connectivity” differs among fields of study. In the context of *migratory* connectivity, a breeding population with high connectivity would have a tight spatial and temporal coupling with a particular wintering area, such that members of the population would rarely mix with members of other populations (Webster et al., 2002). In this study we focus primarily on *population* connectivity, wherein the categorization of high connectivity is conferred upon populations that undergo significant long-term contact with other populations. Our goal is to evaluate the utility of stable isotope ratios as a means of revealing varying degrees of population connectivity by comparing hydrogen stable-isotope ratios with satellite-tracking data from ducks captured at wintering locations in Bangladesh, Hong Kong, and Turkey. Deuterium in rainwater typically becomes more reduced with increased distance from the equator. Hence, we predicted that birds with more northerly breeding and molting grounds would have less deuterium in their feathers. Moreover, increased variation in northward migration flights should be associated with both increased population connectivity (i.e., more widespread intermingling of different breeding populations at the wintering site) and increased variation in hydrogen isotope signatures. This study combines data from stable isotope analyses and from satellite-tracking studies collected from the same set of migratory birds, to provide a rare, but intuitively simple means of testing our predictions.

2. Methods

2.1. Satellite transmitter deployment and feather collection

As part of efforts orchestrated by the United Nations Food and Agriculture Organization and the U. S. Geological Survey, hundreds of satellite tags were deployed in Asia, Eastern Europe,

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