Seasonal movements and migration of Pallas’s Gulls *Larus ichthyaetus* from Qinghai Lake, China

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We studied the seasonal movements and migration of ten Pallas’s Gulls *Larus ichthyaetus* from Qinghai Lake to assess migratory routes and stopover areas. Each individual was captured and equipped with an 18 g solar-powered Platform Transmitter Terminal (PTT) to track its movements from September 2007 to May 2008. Six individuals remained near Qinghai Lake until the PTTs stopped transmitting. Three individuals flew 50–330 km from Qinghai Lake to nearby salt lakes. One individual departed on 8 December and flew over 1,700 km south-west to arrive at coastal Bangladesh on 9 January 2008. Two individuals flew in October to the Brahmaputra River in Assam, India, remaining in the area for at least one month until one stopped transmitting. The second individual travelled south-west to coastal Bangladesh. Of the two individuals overwintering in Bangladesh, one remained for 67 days before migrating north. The second bird departed after 96 days, and it returned to Qinghai on 10 May 2008 after 48 days in migration. Both individuals that overwintered in coastal Bangladesh arrived much later than the outbreaks of Highly Pathogenic Avian Influenza (HPAI H5N1) in poultry in 2007. This disparity in timing would tentatively suggest that this species was not involved in long-distance movements of the virus. Instead, the converse may be true: previous work demonstrates the potential for virus spill-over from poultry into gulls and other wild bird species upon arrival into locations with widespread HPAI H5N1 outbreaks and environmental contamination.

INTRODUCTION

In recent decades, the understanding of bird migration has become of great importance to the conservation of migratory bird species (Boere and Stroud 2006, Li and Mundkur 2007). Declining wetland habitats, human encroachment and emerging diseases seriously threaten the existence of many waterbird species (Li and Mundkur 2007, Olsen et al. 2006). The cross-boundary nature of long-distance migration requires that international strategies be formulated to ensure protection of waterbird species across their geographic ranges (Boere and Stroud 2006).

The lack of information on the timing of migration and stopover areas used during transit by many migratory waterbird species in Asia limits our ability to develop conservation strategies through the annual cycle. Among the waterbirds, gulls (Laridae) are somewhat neglected, with little migration information available, particularly from central and eastern Asia (Li and Mundkur 2007). Asian Waterbird Censuses conducted over much of Asia typically include gulls in their surveys, but since gulls can be highly variable in their ecology and behaviour, they are probably underestimated in these counts. Some gull species are also often involved in or implicated in disease transmission due to their close association with garbage dumps (Muzaffar et al. 2006). An outbreak of Highly Pathogenic Avian Influenza (HPAI H5N1) in Qinghai Lake, China in 2005 resulted in the deaths of over 6,000 waterbirds including over 1,500 gulls of two species (Brown-headed Gull *Larus brunnicephalus* and Pallas’s Gull *L. ichthyaetus*) breeding in the area (Chen et al. 2005, Liu et al. 2005, Chen et al. 2006).

Some information exists on the ecology of Pallas’s Gulls, although their precise migratory routes and seasonal movements are not well known (Ali and Ripley 1991, Li and Mundkur 2007). Information on local movements, and autumn and spring migration of this and other species could also provide some insight into the possibility of wild birds acting as vectors in the epidemiology of avian influenza viruses in the region. Additionally, wild bird movement studies provide information on stopover and wintering areas for better management of threatened species.

To this end, we evaluated the seasonal movements of Pallas’s Gulls from Qinghai Lake, China. The specific objectives of this study were to i) evaluate the seasonal movements of the species at its breeding and wintering areas, ii) delineate the migratory routes of the species along the Central Asian Flyway and iii) identify the stopover areas of the species along its migratory routes.

STUDY AREA

This study was conducted at the Qinghai Lake National Nature Reserve, Qinghai Province, China. Qinghai Lake is located at the north-eastern end of the Qinghai-Tibet Plateau and about 280 km west of the city of Xining in Qinghai Province (Williams 1991, Liu et al. 2004). It is situated at an elevation of 3,193 m above sea level and is the largest saltwater lake in China, with an area of c.526 km². Qinghai Lake is in an endorheic (closed) basin, surrounded by mountains that are the source of its water. Har Lake, a smaller salt lake, is located 200 km north-west of Qinghai Lake and the Qaidam Basin, with a span of >300 km, lies west of Qinghai Lake. Six small islands within Qinghai lake are important breeding areas for Bar-headed Goose *Anser indicus*, Brown-headed Gull *Larus brunnicephalus*, Pallas’s Gull and Great Cormorant *Phalacrocorax carbo*. The lake is frozen for much of the year, opening up briefly during the summer and early autumn (April–October), during which there is rapid growth of vegetation, providing food and breeding habitat for a large numbers of waterbirds. Human activities, particularly the husbandry of yaks and other livestock in the region has created extreme grazing pressure on the surrounding grasslands causing severe degradation of these habitats (Liu et al. 2004).
MATERIALS AND METHODS

We compiled movement data from ten Pallas’s Gulls from Qinghai Lake captured and marked at three sites: Da Lai Quan (37°11′49″N 99°49′38″E), Ha Da Tan (37°07′48″N 99°43′21″E) and shallow ponds near Niao Dao (36°58′51″N 99°52′27″E), all located along the western and north-western edge of Qinghai Lake. We examined local movements of gulls during the post-breeding period and followed their autumn migration chronology and routes from Qinghai Lake to wintering areas in South Asia. Gulls were captured on 14–18 September 2007 using noose-sets. Each noose set consisted of 50–60 loops, and each loop was made of a nylon monofilament attached to a 15 cm-long peg made of bamboo (6 mm diameter). Individual birds were attached around the keel with knots hardened with cyanoacrylate glue. The PTT had a 200 mm long nylon-coated flexible-strap stainless-steel antenna protruding at a 45° angle around the keel with knots hardened with cyanoacrylate glue. The PTT had a 200 mm long nylon-coated flexible-strapped stainless-steel antenna protruding at a 45° angle from the back. Fish bait was placed in the center of the spiral and gulls attempting to reach the bait became entangled in the nooses.

Each bird was weighed, measured and equipped with an 18 g solar-powered portable transmitter terminal (PTT: 9 North Star Science and Technology, LLC, Baltimore, Maryland U.S.A.; and 1 Microwave Telemetry PTT-100, Columbia, Maryland U.S.A.). Each PTT measured 54×20×17 mm (57×30×20 mm for PTT-100) and was attached dorsally between the wings with a harness similar to Dwyer (1972; see Miller 2005). The harness was made of 5 mm wide Teflon® ribbon (Bally Ribbon Mills, Pennsylvania, U.S.A.). The harness consisted of breast and body loops arranged in a spiral radiating outwards from the center. Fish bait was placed in the center of the spiral and gulls attempting to reach the bait became entangled in the nooses.

FILTERING PROGRAM, DCD), although LC 1–3 locations were defined as areas where birds spent more than 50 days between December and April.

RESULTS

We received 2,415 messages from the PTTs, providing a total of 526 locations (Table 1). Only 18.3% of these locations were of LC 1–3 quality; the remaining were LC 0, A, B or Z. One of the PTTs continued providing locations through the spring (until at least 31 May 2008). Two of the tracked individuals were adults (#73023 and #73490) and the rest were juveniles. One of the adults stopped transmitting 7 days after marking while the second adult and two juveniles underwent long-distance migration, making it difficult to compare movement patterns between age classes. Adults and juveniles are therefore lumped together in the summary presented here.

Post-breeding movements

Six birds remained within the vicinity of Qinghai Lake. These birds stayed along the north-western and southern shores, with occasional flights of up to 62 km from the Qinghai Lake vicinity (Fig. 1). For instance one bird

Table 1. Summary of the performance of the Platform Transmitter Terminals that were deployed on ten Pallas’s Gulls from Qinghai Lake in September 2007. Two PTTs were still active as of 31 May 2008.

<table>
<thead>
<tr>
<th>PTT #</th>
<th>Last message</th>
<th>Working days</th>
<th>Overpasses</th>
<th>Total messages</th>
<th>LC 1</th>
<th>LC 2</th>
<th>LC 3</th>
<th>LC 4</th>
<th>Other</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>73023</td>
<td>24 Sep 2007</td>
<td>6</td>
<td>35</td>
<td>53</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>7</td>
<td>8</td>
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<tr>
<td>73484</td>
<td>30 Nov 2007</td>
<td>75</td>
<td>53</td>
<td>104</td>
<td>2</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>15</td>
<td>23</td>
</tr>
<tr>
<td>73486</td>
<td>4 Oct 2007</td>
<td>18</td>
<td>28</td>
<td>54</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>10</td>
<td>11</td>
</tr>
<tr>
<td>73487</td>
<td>2 Dec 2007</td>
<td>77</td>
<td>107</td>
<td>227</td>
<td>1</td>
<td>0</td>
<td>6</td>
<td>11</td>
<td>32</td>
<td>50</td>
</tr>
<tr>
<td>73488</td>
<td>Active</td>
<td>248</td>
<td>241</td>
<td>507</td>
<td>4</td>
<td>7</td>
<td>12</td>
<td>11</td>
<td>104</td>
<td>70</td>
</tr>
<tr>
<td>73489</td>
<td>4 Dec 2007</td>
<td>248</td>
<td>241</td>
<td>526</td>
<td>1</td>
<td>6</td>
<td>11</td>
<td>18</td>
<td>78</td>
<td>114</td>
</tr>
<tr>
<td>73490</td>
<td>22 Mar 2008</td>
<td>189</td>
<td>220</td>
<td>525</td>
<td>1</td>
<td>6</td>
<td>16</td>
<td>24</td>
<td>73</td>
<td>120</td>
</tr>
<tr>
<td>73491</td>
<td>24 Nov 2007</td>
<td>69</td>
<td>97</td>
<td>222</td>
<td>0</td>
<td>1</td>
<td>7</td>
<td>7</td>
<td>41</td>
<td>56</td>
</tr>
<tr>
<td>73492</td>
<td>11 Oct 2007</td>
<td>25</td>
<td>49</td>
<td>114</td>
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<td>5</td>
<td>15</td>
<td>25</td>
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<tr>
<td>73493</td>
<td>22 Oct 2007</td>
<td>36</td>
<td>45</td>
<td>82</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>0</td>
<td>11</td>
<td>15</td>
</tr>
</tbody>
</table>
(#73491) remained within Qinghai Lake for the entire time during which signals were received from the transmitter (Fig. 1). All the birds that remained in the Qinghai Lake vicinity stopped transmitting by 29 November 2007. Birds were frequently located near small waterbodies and river inlets, within 4 km of the lake shore. One bird (#73492) remained near the north-eastern edge of the lake, although on one occasion it moved c.45 km east-south-east of the lake before returning shortly afterwards (Fig. 1).

Two birds (#73486 and #73489) moved >190 km north-west of Qinghai Lake soon after being marked, reaching the site in about 5 days. Bird #73486 flew on 15 September 2007 to an area located 57 km south of Har Lake and about 180 km north of the Qaidam Basin (Fig. 2). Its transmitter stopped on 3 October 2007, 130 km north-west of the Da Lai Quan capture site. On 16 September 2007, #73489 moved 196 km to an area about 60 km south-west of Har Lake, arriving there by 21 September 2007 (Table 2, Fig. 2). It crossed between river tributaries in valleys within an area with a 35 km radius over a period of 20 days. It started moving back towards Qinghai Lake on 10 October 2007 and arrived near the Niao Dao capture site on 12 October 2007. It then flew south-west on 13 October 2007 and arrived at the vicinity of the town of Madoi, about 257 km south-west of the Niao Dao capture site on 16 October 2007. This site was about 10 km east of Ngoring Lake, where it stayed until its signal was lost on 4 December 2007 (Fig. 2).

Automn migration and wintering

Three individuals (#73487, #73488 and #73490) migrated from Qinghai Lake to north-eastern India and coastal Bangladesh, where they overwintered (Fig. 3). Bird #73488 flew south-west from Qinghai Lake on 31 October 2007 to arrive 1,006 km away in Arunachal Pradesh, India, close to the border with the Tibetan Autonomous Region, China, on 4 November 2007. This individual then moved south for c.226 km to arrive in the state of Assam in north-eastern India the following day. It remained within Assam, moving along the Brahmaputra River over a 150 km stretch, and traversing over Kaziranga National Park (Fig. 4). It then started moving farther south-south-west on 11 December 2007 to arrive on 24

Table 2. Migration, stopover locations and duration of stay for four Pallas’s Gulls from Qinghai Lake, China.

<table>
<thead>
<tr>
<th>PTT #</th>
<th>Description and site name</th>
<th>Coordinates</th>
<th>No. of locations</th>
<th>Dates</th>
<th>Duration (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>73487</td>
<td>Migration stopover; Brahmaputra River, Assam, India</td>
<td>27.41°N 94.80°E</td>
<td>31</td>
<td>26 Oct–2 Dec 2007</td>
<td>37</td>
</tr>
<tr>
<td>73488</td>
<td>Migration stopover; Brahmaputra River, Assam, India</td>
<td>27.41°N 94.80°E</td>
<td>34</td>
<td>5 Nov–11 Dec 2007</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>Wintering area; Mouth of Karnaphuli River, Bangladesh</td>
<td>22.22°N 91.82°E</td>
<td>27</td>
<td>24 Dec 2007–13 Apr 2008</td>
<td>112</td>
</tr>
<tr>
<td>73489</td>
<td>Wintering area; Madoi, Qinghai Province, China</td>
<td>34.77°N 98.48°E</td>
<td>97</td>
<td>16 Oct–4 Dec 2007</td>
<td>50</td>
</tr>
<tr>
<td>73490</td>
<td>Migration stopover; Brahmaputra River, Assam, India</td>
<td>27.41°N 94.80°E</td>
<td>5</td>
<td>7 Jan–8 Jan 2008</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>Wintering area; Mouths of the Ganges River, Bangladesh</td>
<td>21.83°N 90.44°E</td>
<td>46</td>
<td>9 Jan–3 Mar 2008</td>
<td>67</td>
</tr>
<tr>
<td></td>
<td>Migration stopover; Mouth of Meghna River, Bangladesh</td>
<td>23.31°N 90.60°E</td>
<td>8</td>
<td>4 Mar–22 Mar 2008</td>
<td>19</td>
</tr>
</tbody>
</table>
December 2007 at southern Patenga region in Chittagong on the south-eastern coast of Bangladesh, close to the opening of Karnaphuli River into the Bay of Bengal. The bird travelled from Qinghai Lake to Bangladesh in 52 days. It remained in the vicinity of coastal Chittagong for the rest of the winter. Individual #43490 flew south-south-west from Qinghai Lake on 8 December 2007 arriving at south-eastern Qinghai province, 377 km away, on 25 December 2007. It then changed direction and flew west-south-west for about 48 km to arrive at the north-western tip of Sichuan province, China. Subsequently, it proceeded to...
south-eastern Tibet, close to the Tibet-India border on 31 December 2007. It then travelled 197 km south-south-west arriving at Arunachal Pradesh, India by 7 January 2008. It flew another 76 km south-west within Arunachal Pradesh before proceeding 671 km south-west to the Bhola region off coastal Bangladesh. This bird eventually arrived in the central coastline of Bangladesh within the Barisal Division on 10 January 2008 and remained within a 25 km radius of the region along the mouth of the Ganges River for the rest of the winter. The total time taken by this bird to travel from Qinghai Lake to Bangladesh was 32 days.
Individual #73487 flew south-south-west from Qinghai Lake on 21 October 2007 and arrived in eastern Tibet, 786 km away. It then moved south-west for 295 km, reaching Assam by 26 October 2007. It moved 150 km along the Brahmaputra River farther upstream from #73488 although there was overlap between their movements. Individual #73487 stopped transmitting on 2 December 2007, when it was in Assam. Two gulls (#73488 and #73490) overwintering in coastal Bangladesh used areas along the edges of major river outlets, mangrove forest patches and paddy fields (Fig. 5).

### Spring migration
Individual #73488 returned to Qinghai Lake after the winter (Fig. 3). It started moving north-west on 30 March 2008. The bird was detected again 148 km north-north-west of Ngoring Lake near Madoi on 9 May 2008. Bird #73490 moved 142 km north-north-east on 27 February 2008 and stopped south of the confluence between the Ganges and Meghna Rivers on 4 March 2008. It then moved up to the Ganges-Meghna confluence the following day, where it remained until last detected on 22 March 2008.

## DISCUSSION
The movement of Pallas’s Gull documented in this study conformed to the Central Asian Flyway reported for both Anatidae and Charadriidae (Boere and Stroud 2006). All three of the birds that migrated to north-eastern India and Bangladesh followed a similar path along the eastern edge of the Central Asian Flyway. This area overlaps broadly with the East Asian Flyway of Anatidae (Miyabayashi and Mundkur 1999) and the East Asian-Australasian Flyway of shorebirds (Brown et al. 2001), although none of the gulls moved south-east from Qinghai Lake, suggesting that they were not following the East Asian Flyway.

Short-distance movements exhibited by some of the marked birds illustrate the importance of salt lakes in the region. The Qinghai Province includes a complex of salt lakes, particularly in western and central Qinghai, along the Qaidam Basin (Williams 1991). These salt lakes are integral to the hydrology defining the landscape and vegetation characteristics of the region. An earlier study suggested that Pallas’s Gulls from Qinghai Lake may stay in these areas for longer periods before moving south for the winter (Zhang et al. 2006, NBBC 2006). In that study one of the two birds that migrated to Bangladesh made a brief stop close to Shiqu in the extreme north-west of Sichuan Province. King and Tai (1991) reported seeing Pallas’s Gulls close to Shiqu and we suggest that they may use river channels for brief stopovers on route to wintering areas.

Two of the three birds that underwent long-distance migration towards Bangladesh stopped along the Brahmaputra River in Assam. These two gulls traversed along the river, remaining in the vicinity for about five weeks. The Brahmaputra River stretch passing through Assam is a significant area for many bird species, migratory and resident alike (Barua and Sharma 1999, Islam and Rahmani 2004). At least seven Important Bird Areas are located immediately adjacent to this stretch of the Brahmaputra (Islam and Rahmani 2004). These habitats are part of the floodplain of the Brahmaputra and contain linkages with surrounding wetland complexes, grasslands and forests making them particularly attractive to waterbirds (Islam and Rahmani 2004, Muzaffar 2004, Muzaffar and Ahmed 2007).

Although one of the two birds spent time in the riparian habitat adjacent to Kaziranga National Park, an internationally significant park (Islam and Rahmani 2004), the species was not reported by Barua and Sharma (1999) in their survey of birds of Kaziranga. Additionally, the Asian Waterbird Census had recorded the species from Tanguar Haor area (part of a freshwater wetland complex in north-eastern Bangladesh) but not from the riparian habitat of the Brahmaputra in Assam (Li and Mundkur 2007). This reflects the importance of telemetry studies for identifying areas used by species at certain times of the year that can potentially be missed by standard bird surveys.

The shoreline of the Brahmaputra River and surrounding freshwater wetlands in Assam may serve as important stopover areas for Pallas’s Gulls heading further south towards the Bay of Bengal. Our study and an earlier report (NBBC 2006) found similar movements of birds that arrived in Bangladesh to overwinter. However, in the earlier study, the stopover area for one of the marked birds was at Zhaling Lake, adjacent to Ngoring Lake near Madoi, where it stayed for slightly less than two months before migrating south-west to Bangladesh (NBBC 2006). The second bird in that study moved to Keuken Lake 118 km south-west of Har Lake where it stayed for almost three months before migrating south to Bangladesh. Stopover areas of Pallas’s Gulls from the Qinghai Lake region, therefore, are very widespread and presumably depend on age of the birds, food abundance and weather patterns.

The six birds in our study that were tracked in the vicinity of Qinghai may well have migrated south after we lost their transmitter signals. The two gulls that overwintered in the coastal areas of Bangladesh remained in two distinct areas. One was located in the central coastline of Bangladesh near Bhola and Barisal districts, where replanted mangroves form the dominant vegetation (NCSIP 1999), while the other spent most of its time in the vicinity of the Patenga region of Chittagong, close to a commercial sea port. Large numbers of Pallas’s Gulls are reported regularly from both these areas, but especially the central region (Lopez and Mundkur 1997, Khan 2005, Rasmussen and Anderton 2005, Li and Mundkur 2007), and it is likely that a high proportion of these birds are from the Qinghai Lake region. The coastal mudflats and mangrove patches are important wintering habitats for Pallas’s Gulls. Large numbers of shorebirds, other gulls and ducks are also recorded regularly from these areas (Lopez and Mundkur 1997, Li and Mundkur 2007). One of our gulls started its return trip to the north along the river delta west of Har Lake, while the other moved south-west to Bangladesh (NBBC 2006). The bird was detected again 148 km north-north-west of Har Lake on 21 October 2007 and arrived in eastern Tibet, 786 km away. It then moved south-west for 295 km, reaching Assam by 26 October 2007. It moved 150 km along the Brahmaputra River farther upstream from #73488 although there was overlap between their movements. Individual #73487 stopped transmitting on 2 December 2007, when it was in Assam. Two gulls (#73488 and #73490) overwintering in coastal Bangladesh used areas along the edges of major river outlets, mangrove forest patches and paddy fields (Fig. 5).

### Implications for avian influenza
Wild waterbirds act as reservoirs of many different avian influenza viruses (categorised into subtypes) that usually cause minor or no disease symptoms in wild waterbirds or domestic poultry and are termed Low Pathogenicity Avian Influenza (LPAI) viruses (Webster et al. 2006, Swayne 2008). HPAI viruses have emerged historically in different poultry from LPAI precursors (Webster et al. 2006, see Swayne 2008 for a review). Avian influenza...
The virus of the subtype H5N1 first emerged as an HPAI in poultry in 1997 in Hong Kong from LPAI H5N1 virus precursors. This virus circulated and disseminated in poultry initially in east and south-east Asia, subsequently spreading to Europe and parts of Africa and resulting in massive poultry culls to help contain its spread (Muzaffar et al. 2006, Webster et al. 2006, Swayne 2008). The first outbreak of HPAI H5N1 in wild waterbirds in the absence of poultry occurred in 2005 in Qinghai Lake, and demonstrated the susceptibility of multiple wild migratory bird species to the disease (Chen et al. 2005, 2006).

The first officially reported outbreak of HPAI H5N1 in Bangladesh was on 22 February 2007 (FAO 2008) but it is likely that the virus was circulating prior to this date as the first symptoms were noted on 5 February 2007 (OIE 2007, 2008, WHO 2008). In total, 221 confirmed cases were reported in Bangladesh and the rapid spread of the virus was most likely a result of little or no biosecurity in the country’s poultry network (FAO 2008). During initial outbreaks, feral crows tested positive for HPAI H5N1 as a result of feeding on infected dead chickens left out in the environment (FAO 2008). Environmental contamination through improper disposal of carcasses, eggs, or faecal material is thought to be a major route by which the virus is exchanged among poultry and wild birds (FAO 2007).

The first Pallas’s Gull in our study that overwintered in Bangladesh arrived on 24 December 2007 while the second arrived on 10 January 2008. By this time, HPAI H5N1 was probably endemic and had infected approximately one third of all districts in Bangladesh (FAO 2008, OIE 2007, 2008). We are unable to determine whether migrating gulls, or other species could have introduced HPAI H5N1 into Bangladesh during southern migration from the Qinghai Lake region into Bangladesh in the autumn or winter of 2005 following the outbreak in Qinghai Lake. Similarly, we do not know whether migration could have introduced HPAI H5N1 virus in 2006, although significantly fewer wild bird cases were reported for Qinghai Lake that year. It is important to note that the movement of gulls or other migratory species into a region experiencing widespread poultry outbreaks demonstrates how the HPAI H5N1 virus has the potential to spill over from the poultry sector into wild bird species, then enabling further spread or spatial movement of the virus. This may also help explain persistence of the HPAI H5N1 virus in locations where poultry and wildlife species are in regular close contact.

Further studies combining virological assessment of wild birds with telemetry studies to determine timing and duration of migration may help better explain the epidemiology of HPAI H5N1. Additionally, surveillance of wild birds and domestic poultry for both LPAI and HPAI viruses combined with telemetry studies to determine extent and duration of overlap in the ecology of wild and domestic birds are necessary to help determine the risk of infecting wild birds with viruses from poultry and vice versa.

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