Spring Migration Routes of Mallards (Anas platyrhynchos) that Winter in Japan, Determined from Satellite Telemetry

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Wild birds, in particular waterfowl, are common reservoirs of low pathogenic avian influenza viruses, and infected individuals could spread the viruses during migrations. We used satellite telemetry to track the spring migration of the mallard ducks (*Anas platyrhynchos*) that winter in Japan. We studied their migration routes, distribution of stopover and breeding sites, and timing of migration movements. We tracked 23 mallards from four different wintering sites. Nine of the 23 mallards reached presumable breeding sites, where migration terminated. The migration routes of the birds greatly differed not only among the wintering sites but also within the same wintering site, although the general feature of the routes was shared among birds within the same wintering site. The mallards used several stopover sites, and they typically stayed for a long period (about one to four weeks) at a site between migration intervals of two to three days. Stopover sites were located in northeast Japan, the eastern coastline of South Korea and North Korea, and the interior of Far Eastern Russia. Mallards from three different wintering sites used a stopover area near the middle part of the Ussuri river in Russia. The terminal sites, which were presumably also breeding sites, were distributed widely over northeast Asia and Far Eastern Russia. These results suggest that mallards that winter in Japan originate from breeding areas widely distributed across eastern Asia. Mallards could potentially transmit avian influenza viruses between Japan and a broad region of northeastern Asia.

Key words: spring migration route, satellite-tracking, Mallard, *Anas platyrhynchos*, avian influenza

INTRODUCTION

Wild birds, in particular waterfowl, play a role on the circulation of influenza A virus. They often carry lowly pathogenic avian influenza (LPAI) viruses (Alexander, 2000; Munster et al., 2005; Olsen et al., 2006), and infected individuals could spread LPAI viruses over a wide area, since many waterfowl migrate long distances between the breeding and wintering grounds. Migratory waterfowl may also carry highly pathogenic avian influenza (HPAI) viruses which pose a risk for interspecific transmission into poultry, typically resulting in high mortality and requiring the culling of infected flocks (Liu et al., 2005; Olsen et al., 2006). Furthermore, in Asia wild birds are now suspected of spreading of the highly pathogenic H5N1 avian influenza virus over long distances through migration (Li et al., 2004; Chen et al., 2006).

To understand the current circulation mechanism of LPAI/HPAI viruses, we need to study the movements, distribution, and abundance of host species, as well as the ecology, life history, and phylogeography of the viruses. Although there have been many phylogeographical and ecological studies of LPAI viruses and many reports on the

prevalence of LPAI/HPAI (e.g., de Jong et al., 1997; Delogu et al., 2003; Hatchette et al., 2004; Gilbert et al., 2006; Olsen et al., 2006; Munster et al., 2007), there has been little research on the movement patterns of waterfowl, particularly in eastern Asia. This prevents us from fully understanding the epidemiological system of LPAI/HPAI, and results in unsound speculation regarding the role that wild birds and their wetland habitats may play in the spread of influenza viruses.

Avian influenza viruses spread in several possible ways, including movements of infected poultry, re-use of inadequately cleansed transportation crates, commercial trade in caged wild birds, and migration movements of wild birds (Birdlife International, 2007). However, it is still not clear which of these pathways play an important role in the spread of HPAI viruses. To evaluate the potential role of wild birds in the circulation of HPAI, it is important to know the migration routes of waterfowl such as ducks. The prevalence of HPAI in the ducks and the degree of their interaction with poultry such as domestic ducks should then be examined for each stopover site. Little is known, however, about the migration of waterfowl in East Asia, where HPAI outbreaks in poultry have already occurred in many areas, including Japan (Li et al., 2004; World Health Organization, 2007).

Satellite tracking is a powerful technique for studying bird migration because it allows tracking of individual birds worldwide (Cohn, 1999; Webster et al., 2002; Higuchi and Pierre, 2005). Via satellite-tracking studies, scientists have enhanced their understanding of avian migratory pathways (e.g., Higuchi et al., 1996, 1998, 2004, 2005; Kanai et al 2002; Fox et al., 2003; Meyburg et al., 2003) and migratory behaviors or strategies (e.g., Hake et al., 2003; Ueta and Higuchi, 2002; Thorup et al., 2003).

We used satellite telemetry to track mallard ducks (*Anas platyrhynchos*) that winter in Japan during their spring migration to East Asia. The mallard is one of the most abundant waterfowl in the world, and Munster et al. (2005) detected numerous influenza A virus subtypes, including the varieties H5 and H7, which may sometimes be highly pathogenic, in this species. In this paper, we report the spring migration routes, distribution and habitat at stopover and breeding sites, and movement patterns of mallards through time. The results reported here are not directly related to the understanding of the observed spread of HPAI avian influenza viruses, but provide basic information on the migration of a duck species that may carry the viruses. We also demonstrate the importance of Japanese winter habitats to mallards that nest over a broad region of eastern Asia, and identify important stopover areas used by mallards during migration. An understanding of linkages between wintering, migration, and nesting habitats is critical in developing conservation plans for migratory waterfowl.

MATERIALS AND METHODS

Satellite tracking

In the 2005–2006 and 2006–2007 wintering seasons, we captured a total of 65 mallards at four widely separated wintering areas in Japan; (1) Obihiro (42°56'N, 143°18'E), Hokkaido Prefecture, (2) Saitama Imperial Wild Duck Preserve (42°58'N, 139°43'E), Saitama Prefecture, (3) Sasebo Zoological Park and Botanical Garden (33°12'N, 129°42'E), Nagasaki Prefecture, and (4) Sadohara (32°02'N, 131°29'E), Miyazaki Prefecture (Table 1). Distances between capture sites ranged from 270–911 km. We captured these birds harmlessly by using ring nets and flat net traps.

We attached satellite transmitters (platform transmitter terminals [PTTs]) to the back of the birds with a harness system. The harness consisted of two Teflon-treated ribbons sewn to an attachment point at the anterior end of the PTT. The ribbons crossed beneath the bird's breast, where they passed through a small tube at the keel of sternum, and were sewn together with a nylon thread. The ribbons were then sewn to an attachment point at each corner of the posterior end of the PTT. We expected that the PTTs would fall off when the thread deteriorated two or three years after attachment. We used solar- and battery-powered PTTs (Models 16GS and 20GS, respectively; North Star Science and Technology) that weighed 20 g, and were 50×20×17 mm in size, with a 198-mm antenna. We also used 12-g solar powered PTTs and 30-g Argos GPS PTTs (Microwave Telemetry) that were 43×18×14 mm and 62×22×21 mm in size, respectively, with a 178-mm antenna. At the time of capture, birds ranged from 880–1450 g in body weight. The weight of a PTT plus harness was only 1.2–3% of the body weight of the birds.

The PTT locations were estimated by the Argos system (Argos, 1996) and were reported as latitude and longitude (WGS84 datum), with location times recorded as Greenwich Meridian Time (GMT). Argos classified the location accuracy (location class, LC) into 3, 2, 1, 0, A, B, and Z. The standard deviation of positional error on the latitudinal and longitudinal axes was <150 m for LC 3, 150–350 m for LC 2, 350–1000 m for LC 1, and >1000 m for LC 0; the location accuracy for LCs A, B, and Z could not be determined. Since other studies have reported that the approximate accuracy of LC 0 is within 10 km (Bothers et al., 1998; Britten et al., 1999; Hays et al., 2001), the standard deviation may have been less than 5 km for LC 0. We used the locations of LCs 0 to 3 to determine the migration routes of marked mallards. Since mallards move thousands of kilometers during migration, location errors of <10 km were negligible.

Table 1. Capture sites, date of capture, and number of male and female mallards deployed with PTT. In the column for success rate of tracking, sets of three numbers indicate birds that were successfully tracked to their terminal sites / birds that were tracked at least partially / birds that were deployed with PTT.

Capture site	Capture date (m/d/y)	Success rate of tracking		Total birds deployed with PTT
		males	females	
Obihiro	12/16/05, 11/08/06	0 / 0 / 19	0 / 1 / 6	25
Saitama	01/31/05, 12/26/06–01/05/07	3 / 3 / 7	1 / 5 / 9	16
Sasebo	03/12/07–03/14/07	1 / 5 / 6	2 / 2 / 3	9
Miyazaki	11/12/06–02/23/07	2 / 4 / 8	1 / 7 / 7	15

Statistical analyses

We determined departure dates at wintering sites, and determined arrival dates, departure dates, and duration of stays at stopover sites. Because locations of some PTTs were intermittent, we could not always determine exact departure or arrival dates. When the exact date of a migration movement could not be determined, we used the central date in the range of possible dates. If there were an uneven number of days in the potential range, we used the later of the two most central dates. We did not estimate arrival or departure dates if the potential range of dates was >5 days.
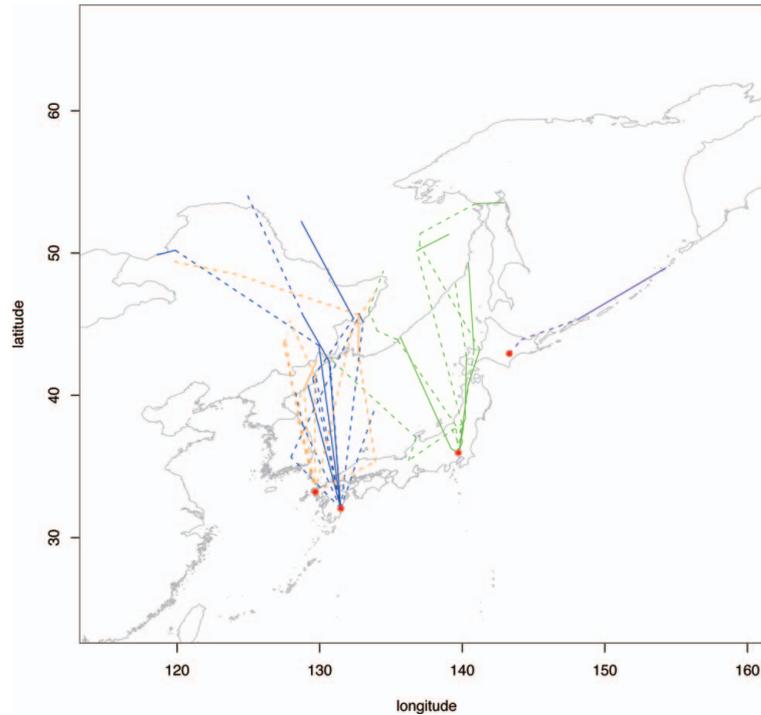

Fig. 1. Spring migration routes of mallards marked with satellite radio transmitters at four wintering sites in Japan. Red circles indicate wintering sites (from north to south, Obihiro, Saimata, Sasebo, and Miyazaki). The routes of mallards from different sites are indicated by purple (Obihiro), light green (Saitama), orange (Sasebo), and blue (Miyazaki). When the time interval between two adjacent PTT locations was more than two days, the segment is shown by a dotted line.
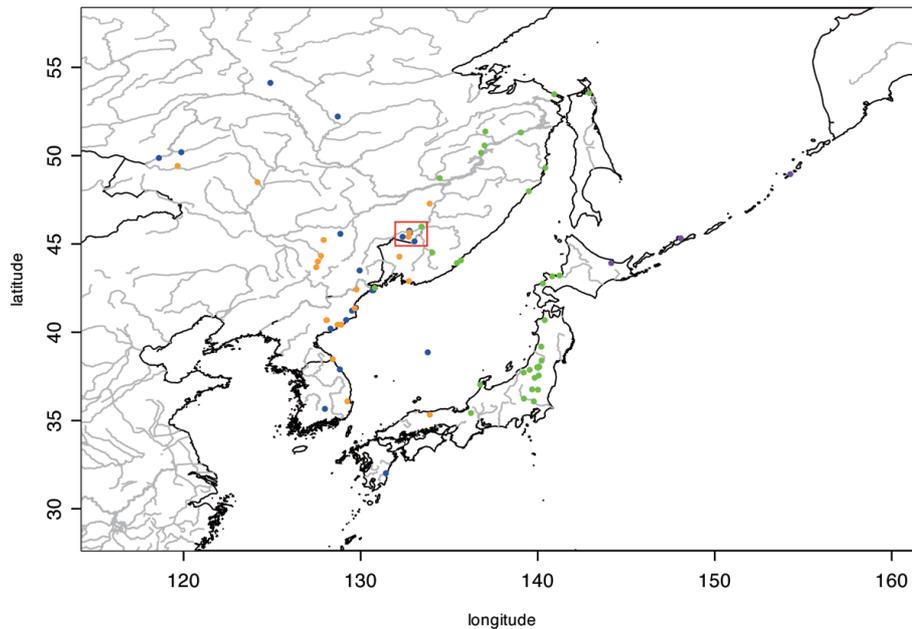

Fig. 2. Distribution of stopover sites of mallards during spring migration from Japan. Large rivers are shown with grey lines. The color of a point indicates the wintering site of the bird that used the stopover site (purple, Obihiro; green, Saitama; orange, Sasebo; blue, Miyazaki). Red box indicates stopover areas shared by mallards from different wintering sites.

A stopover site was defined as an area used after departure from winter area, and where a mallard did not travel in one particular direction (i.e. it exhibited a more or less random movement pattern) for at least 24 h. We obtained the coordinates of a stopover site by calculating the centroid of PTT locations for the site. If a PTT location had no adjacent location for more than 24 h, we did not classify it as a stopover site, because we could not distinguish between a bird actually staying at a single location and signals being scarce around the location. A terminal site was defined as the last site at which a bird stayed for more than one month. We expect that most terminal sites also represented breeding and molting sites of the tracked birds. Because the duration of incubation is 27 or 28 days for mallards (Cramp et al. 1985), females had to stay at a terminal site for more than a month for it to be considered a nesting site. Although most males do not care for their eggs or chicks, they also stay at breeding sites and molt their plumage (Cramp et al., 1985), so we also considered that males that spent >1 month at a terminal site were breeding.

The travel distance from one site to the next was calculated as the geodesic distance between two coordinates on the ellipsoid, using Vincenty's inverse formulae (Vincenty, 1975). We calculated the mean duration of stopover intervals throughout migration by averaging the mean number of days each bird remained at its various stopover sites (for example, four means of staying durations in various stopover sites were obtained from the four birds released at Miyazaki, and then a mean of the four means was calculated). Obvious outliers were excluded from calculations, but the values for the outliers are reported in the results. All calculations were carried out using R 2.6.0 (R Development Core Team, 2007).

RESULTS

Migration routes

We tracked migration routes for 27 of the 65 mallards to which we attached PTTs (Table 1, Fig. 1). Thirty-eight of the PTTs stopped functioning for unknown reasons shortly after the birds were released. Of the 27 mallards that departed winter sites with functional PTTs, 10 birds completed migration to terminal sites, whereas 17 PTTs stopped functioning during migration (Table 1). Some birds may have been shot by hunters.

Migration routes differed greatly, not only among individuals from different wintering sites but also among individuals from the same wintering site, although mallards from the same wintering sites followed the same general migration routes. The only mallard that departed from Obihiro with a functional PTT moved along Kuril Islands and almost reached Kamchatka Peninsula, before the PTT stopped transmitting near Onekotan Island. Six mallards from

Saitama traveled northward and crossed the Sea of Japan, although the route taken by some individuals was uncertain because those birds moved long distances between transmissions. All six of the birds reached the southeastern area of Far Eastern Russia. One male ended its spring migration in Niigata Prefecture, Japan (about 210 km north of the original site). The mallards from Sasebo and Miyazaki traveled northward, and most crossed the Sea of Japan just like the mallards from Saitama. However, some birds went north along the eastern coastline of the Korean Peninsula. Most birds stayed around the border between North Korea and China. One bird from Sasebo and two birds from Miyazaki moved farther inland and reached points near the borders between Nei Monggol, China, and Russia (one from Sasebo and one from Miyazaki, ca. 49°N, 118°E; the other from Miyazaki, ca. 54°N, 125°E) (Fig 1). In some cases, birds exhibited a sharp change in direction during migration. A mallard from Sasebo moved northward from the north end of the coastline of North Korea, reached the border between Russia and China in northern Heilongjiang Province (45°39'N, 132°45'E) after crossing the Sea of Japan directly, and then turned sharply west and finally arrived at the border between Russia and China in southern Chitinskaya (49°25'N, 119°37'E). A bird from Saitama reached northern Khabarovsk (51°22'N, 137°02'E), and then turned east and reached the north end of Sakhalin Island.

Migration schedule and movement pattern

The estimated departure dates from wintering sites and the arrival dates at terminal sites differed greatly among individuals and ranged over several months, even among birds that had wintered at the same site (Table 2). The tracked mallards stopped at several locations during migration (Fig. 2). For those that reached terminal sites, the mean number of stopover sites was 3.00, 2.00, and 1.33 for birds from Saitama, Sasebo, and Miyazaki, respectively. Mallards typically stayed for a long time (about one to four weeks) at one site between short travel periods of around two or three days (Fig. 3, Table 2).

Distribution of stopover sites and terminal sites

Stopover sites were scattered around northeastrtn Japan, the eastern coastline of South Korea and North Korea, and the interior of Far Eastern Russia (Fig. 2). Stopover sites were often located near coastlines or along the

Table 2. Range of departure dates from the four wintering sites, arrival dates at terminal sites, mean duration (± SD) birds were in migration between two stopover sites, mean duration (±SD) in staying at stopover sites, and mean number (±SD) of stopover sites. The calculation method for each statistics is described in Methods. Numbers in parentheses indicate sample sizes. We could not estimate departure dates at Obihiro and Sasebo, because departures occurred on an unknown date over a period of more than 5 days. No birds tracked from Obihiro completed their migration. When calculating mean travel durations, we eliminated outliers of 36 days for Saitama and 61 days for Miyazaki that probably resulted from our failure to detect stopover sites due to missing locations for some days.

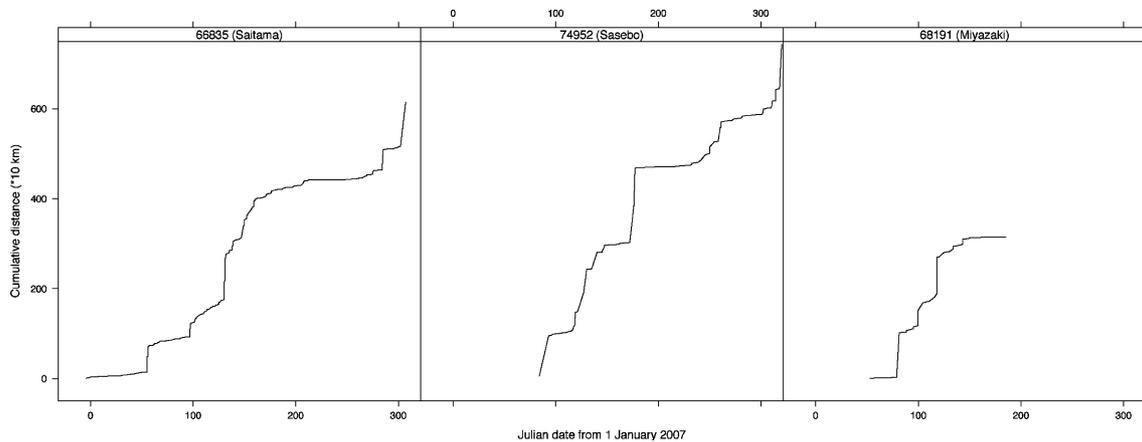| Capture site	Departure date from capture site	Arrival date at terminal site	Duration of migration (days)	Duration at stopover sites (days)	Number of stopover sites
Obihiro	–	–	1.67 (1)	4.5 (1)	–
Saitama	2/25/06–4/15/06 (4)	5/4/06 (1)			
	5/10/07 (1)	5/1–6/10 (3)	2.64±1.26 (8)	17.60±7.98 (8)	3.00±2.45 (4)
Sasebo	–	4/17, 5/23 (2)	2.08±0.38 (3)	19.38±0.88 (2)	2.00±1.73 (3)
Miyazaki	3/16–4/20 (8)	4/15, 4/30 (2)	3.15±1.71 (8)	27.81±15.97 (4)	1.33±0.82 (4)

Fig. 3. Relationships between date (Julian days from 1 January) and cumulative distance (10^3 km) for mallards marked with satellite radio transmitters that migrated from wintering sites in Japan. Results are shown for individuals 66835 (wintered at Saitama), 74952 (wintered at Sasebo), and 68191 (wintered at Miyazaki). These birds reached the terminal sites of their migration.
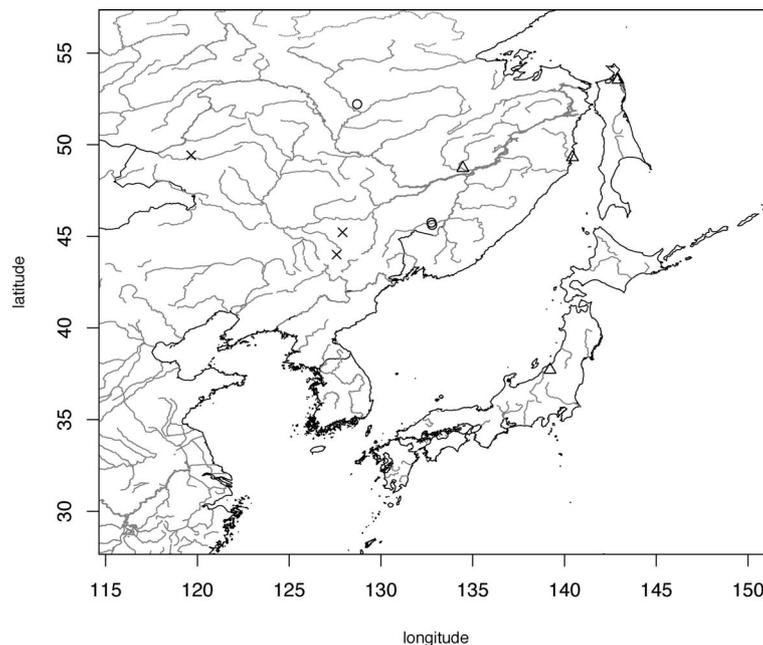

Fig. 4. Distribution of terminal sites (presumed breeding sites). Large rivers are shown wtih grey lines. Each symbol indicates the wintering site of a bird that arrived at a terminal site (△: Saitama; ×: Sasebo; ○: Miyazaki).

basins of large rivers. Both of the birds from Sasebo and those from Miyazaki stopped over on the coast of North Korea. Mallards from Saitama, Sasebo, and Miyazaki each used stopover locations at Ozero Chanka Lake and the middle part of the Ussuri river around the boundary of China and Russia (45°–46°N, 132°–134°E).

The terminal sites, which were presumably breeding sites, were distributed widely across northeastern Asia and Far Eastern Russia, and in most cases were located along the basins of large rivers similar to the stopover sites (Fig. 4). The distribution of terminal sites seemed to differ among birds from different wintering sites. The terminal sites of

Sasebo birds were the farthest westward, those of Saitama birds were the farthest eastward, and those of mallards from Miyazaki lay between these regions. However, we could not carry out a statistical analysis due to the small sample size.

DISCUSSION

We tracked the spring migration of 27 mallards from the four wintering sites in Japan. After departing Japan, many of the birds crossed the Sea of Japan directly and reached the coastline of North Korea. It was expected that ducks wintering in Kyushu Island would travel through the Korean Peninsula in migration; however, most did not. Instead most

bypassed the Korean Peninsula by migrating across the Sea of Japan, or followed the coastline of Korea. Although mallards from Kyushu typically moved farther westward than birds marked on Honshu or Hokkaido, there was considerable overlap between the two, and there were individual differences among birds from the same wintering area. Although we could not determine the terminal sites of migration for some of the tracked birds, those that we did follow to the conclusion of their migration suggest that mallards that winter in Japan originate from breeding sites widely scattered around the interior of northern China and Far Eastern Russia. The stopover sites were also distributed over a broad range. However, we emphasize that some stopover sites were used by birds from widely separated wintering sites (Saitama, Sasebo, and Miyazaki; the distance from Saitama–Sasebo is 969.5 km; Sasebo–Miyazaki, 211.7 km; Miyazaki–Saitama, 876.3 km). Mallards from both Honshu and Kyushu used the same stopover locations on Khanka Lake and the middle portion of the Ussuri River. This indicates that the migration routes of the mallards that winter in Japan form a complex network in Asia, and that the individuals from different wintering sites use some common stopover sites during migration.

Mallards employed a "long-stay and short-travel" migration strategy. Individuals typically had long stopovers of several weeks between trips of two or three days. Because mallards always employ powered flights and have heavy body weight relative to wing area, their flights would consume considerable energy (Kelinger, 1995). Long stopovers are likely necessary to replenish energy reserves used during migration. Our data indicate that it takes several weeks to replenish the energy reserves consumed by a trip. This migration pattern is different from that of hawks such as grey-faced buzzards (*Butastur indicus*) and Oriental honey-buzzards (*Pernis ptilorhyncus*) (Higuchi et al., 2005; Shiu et al., 2006). These raptor species can travel for long distances by using soaring flight, and thus exhibit a "short-stay and long-travel" migration strategy.

Although band-recovery data for mallards marked in Japan are available from 1961 (Yamashina Institute for Ornithology, 2002), we had little information on mallard stopover sites, possible breeding sites, or movement patterns during migration in Asia. Band-recovery data merely connected release and recovery locations, and most recoveries were likely mallards shot by hunters in Russia (Yamashina Institute for Ornithology, 2002). The present study is the first that reports the details of migration routes, distribution of stopover sites, possible breeding sites, and movement patterns of mallards from different wintering sites in Japan.

Our results are important in understanding the breeding distribution of mallards that winter in Japan and in identifying their major migration habitats. Our findings also contribute to understanding the transmission of avian influenza viruses. The migration routes of the mallards suggest a complex network, in which birds from different wintering areas co-occurred at some stopover sites. Thus, mallards could contribute to the wide occurrence of the lowly pathogenic avian influenza and the current or future spread of the highly pathogenic avian influenza through fecal-oral transmission at shared stopover areas (Webster, 1992). The viruses may disperse from "hub" stopover sites to various other sites.

Our data on the migration routes, stopover sites, and movement rates of mallards will be useful in predicting the range and speed of the spread of LPAI/HPAI viruses, although some other information is needed to evaluate these data, e.g., the degree of interaction between waterfowl (and their feces) and poultry, inter- and intraspecific infectivity of LPAI/HPAI, and the incubation period and survival rate of HPAI infected birds. The frequency of HPAI outbreaks detected in Asia has increased in the last decade. Thirteen countries in Asia have confirmed the occurrence of HPAI (subtype H5N1) in poultry and wild birds such as the bar-headed goose (*Anser indicus*), the great black-headed gull (*Larus ichthyaetus*), and the brown-headed gull (*Larus brunnicephalus*) since 2003 (Liu et al., 2005; World Hearth Organization, 2007). Because the precursor genes of future pandemic influenza viruses are perpetuated in ducks that nest in Siberia (Okazaki et al., 2000), studies on waterfowl migration, and the life history and phylogeography of avian influenza viruses, should rapidly be initiated in Asia.

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