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RESEARCH ARTICLE

Tracking domestic ducks: A novel approach for documenting poultry market chains in the context of avian influenza transmission

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Abstract

Agro-ecological conditions associated with the spread and persistence of highly pathogenic avian influenza (HPAI) are not well understood, but the trade of live poultry is suspected to be a major pathway. Although market chains of live bird trade have been studied through indirect means including interviews and questionnaires, direct methods have not been used to identify movements of individual poultry. To bridge the knowledge gap on quantitative movement and transportation of poultry, we introduced a novel approach for applying telemetry to document domestic duck movements from source farms at Poyang Lake, China. We deployed recently developed transmitters that record Global Positioning System (GPS) locations and send them through the Groupe Spécial Mobile (GSM) cellular telephone system. For the first time, we were able to track individually marked ducks from 3 to 396 km from their origin to other farms, distribution facilities, or live bird markets. Our proof of concept test showed that the use of GPS-GSM transmitters may provide direct, quantitative information to document the movement of poultry and reveal their market chains. Our findings provide an initial indication of the complexity of source-market network connectivity and highlight the great potential for future

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telemetry studies in poultry network analyses.

Keywords: avian influenza, domestic duck, market chain, network, poultry, telemetry

1. Introduction

Avian influenza (AI) is an infectious disease of poultry and wild birds caused by type A influenza viruses, and these viruses are classified as low pathogenic (LPAI) or highly pathogenic (HPAI) depending on their virulence in domestic chickens (FAO 2007). Wild waterbirds may serve as natural hosts or reservoirs for LPAI viruses that do not commonly cause severe clinical symptoms (FAO 2007; Lebarbenchon *et al.* 2010). In contrast, HPAI viruses of subtypes H5 and H7 may infect poultry and cause disease outbreaks and socio-economic impacts in communities with poultry farming (FAO 2007; Lebarbenchon *et al.* 2010). HPAI viruses seem to arise in artificial ecosystems including poultry farms, free-ranging duck production areas, and live bird markets (LBMs) rather than in natural ecosystems (Lebarbenchon *et al.* 2010). Migratory wild ducks may have potential to transmit the virus during migration by shedding viruses after survival from infection or while asymptomatic (Chen *et al.* 2006; Gaidet *et al.* 2010; Cappelle *et al.* 2014), but HPAI is mainly referred as a disease of domestic poultry that spreads and persists within artificial systems (Gilbert *et al.* 2007, 2008; Lebarbenchon *et al.* 2010).

The Asia-Pacific region has been regarded as an epicentre of new emerging infectious diseases because of the high human densities, intensive livestock production with limited biosecurity, and close association of livestock and human habitation (Shortridge and Stuart-Harris 1982; Jones *et al.* 2008; WHO 2011). Southern China has been suggested as a hotspot for novel AI emergence and pandemic risks (Webster *et al.* 2006; Jones *et al.* 2008; Fuller *et al.* 2013), and HPAI H5N1 emerged in southern China (Li *et al.* 2004; Chen *et al.* 2006; FAO 2007; WHO 2015) in an area where rice farming provides feeding habitat for both free-grazing domestic ducks as well as wild and migratory birds (Takekawa *et al.* 2010). Domestic ducks are believed to be the most important hosts that shed HPAI (Sturm-Ramirez *et al.* 2005; Gilbert *et al.* 2007, 2008), and high densities of free-grazing domestic ducks have been associated with HPAI H5N1 persistence and transmission (Olsen *et al.* 2006; Gilbert *et al.* 2007, 2008; Xiao *et al.* 2007; Cappelle *et al.* 2014).

To better understand the transmission risks of HPAI, information is needed on spatial distribution and movements of three key components: wild birds, poultry, and humans. Poyang Lake, the largest freshwater lake in China, has all of the risk factors for transmission (Gilbert *et al.* 2007, 2008; Takekawa *et al.* 2010; Wang *et al.* 2013; Cappelle *et al.* 2014), but detailed agro-ecological conditions associated with HPAI spread and persistence are still largely unknown (Gilbert *et al.* 2007). While agricultural summaries and local statistics have been used to derive information on the distribution of poultry (Wang *et al.* 2013; Cappelle *et al.* 2014), little information exists on the movements of poultry from farms in this region to the markets where they are sold (but see Martin *et al.* 2011b).

Most poultry are sold through LBMs in southern China, and concerns about LBMs in the epidemiology of HPAI have increased since the first report of human H5N1 infection in Hong Kong (Webby and Webster 2001). In LBMs, live poultry from large catchment areas are intermixed, and the birds are traded to other markets that results in a network of trade connections (Gilbert *et al.* 2014). These networks favor persistence of virulent strains with continuous circulation of avian influenza viruses between connected farms or markets (Lebarbenchon *et al.* 2010; Fournié *et al.* 2013). Several studies have explored poultry movements through market chains in Cambodia (Van Kerkhove *et al.* 2009; Fournié *et al.* 2012), Vietnam (Soares Magalhães *et al.* 2010; Fournié *et al.* 2012, 2013), and China (Martin *et al.* 2011b) through use of indirect methods including interviews and questionnaires. However, very little information has been available from direct documentation of poultry movements from source producers through their market chains in this region.

In the past few decades, Global Position System (GPS) telemetry has been used as an effective tool for tracking detailed movements of wild animals in remote or inaccessible areas. Satellite transmitters also have been used in studies of wild birds in AI studies (FAO 2007; Takekawa *et al.* 2010; Cappelle *et al.* 2014), but only one previous study has applied transmitters on poultry (Prosser *et al.* 2015), and those were short-duration loggers (2–3 days) that required recapturing the birds on the farms where they were marked. In this study, we introduced a novel application to mark domestic ducks with recently-developed transmitters that use the Global System for Mobile Communications or Groupe Spécial Mobile (GSM) to transmit GPS high-quality location data without requiring recovery of marked individuals. We hypothesized that this new technology would allow us to track individual domestic ducks moving through a market chain system from source farms to distribution centers, markets, and potentially end-users. We proposed a field study as a proof of concept to document the movement of poultry and identify the market chains emerging from the Poyang Lake region.

2. Materials and methods

2.1. Study area

Poyang Lake is the largest freshwater lake in China with extensive wetland ecosystems reaching up to ca. 4 000 km^2 in the flooding season (Qian *et al.* 2011). It is located at the middle reaches of the Yangtze River and is freely connected to the river in the north (Fig. 1). As a southern terminus and major wintering grounds for wild waterfowl in the East Asian Flyway, about 425 000 waterbirds (ranging from 298 000 to 726 000 in 2003–2008) comprised of ca. 60 species annually visit Poyang Lake during the winter (Qian *et al.* 2011). The lake and its watershed also are well-recognized as a wetland of international importance for its conservation value in hosting internationally threatened wild migratory waterbirds (Qian *et al.* 2011). At the same time, this area supports approximately 10 million people and more than 14 million poultry raised by traditional husbandry and traded through LBMs (Takekawa *et al.* 2010; Wang *et al.* 2013; Cappelle *et al.* 2014). These unique environments serve as a melting pot of humans, wild waterbirds, and domestic poultry, establishing Poyang Lake as a key area of concern for several strains of avian influenza transmission at the wild bird-poultry interface including: H5N1 in poultry and wild birds (Martin *et al.* 2011a; Prosser *et al.* 2013), H5N1 and H3N2 in humans (Fuller *et al.* 2013), H7N9 in humans and poultry (Gilbert *et al.* 2014), and H10N8 in humans (García-Sastre and Schmolke 2014). For this study, we worked with poultry farmers in the southern and southwestern regions of Poyang Lake where poultry and wild birds are more abundant and may commonly interact. We visited five counties and three cities around the lake; these were Nanchang, Jinxian, and Xinjian counties near Nanchang City, Yugan County near Shangrao City, and Yongxiu County near Jiujiang City (Fig. 1).

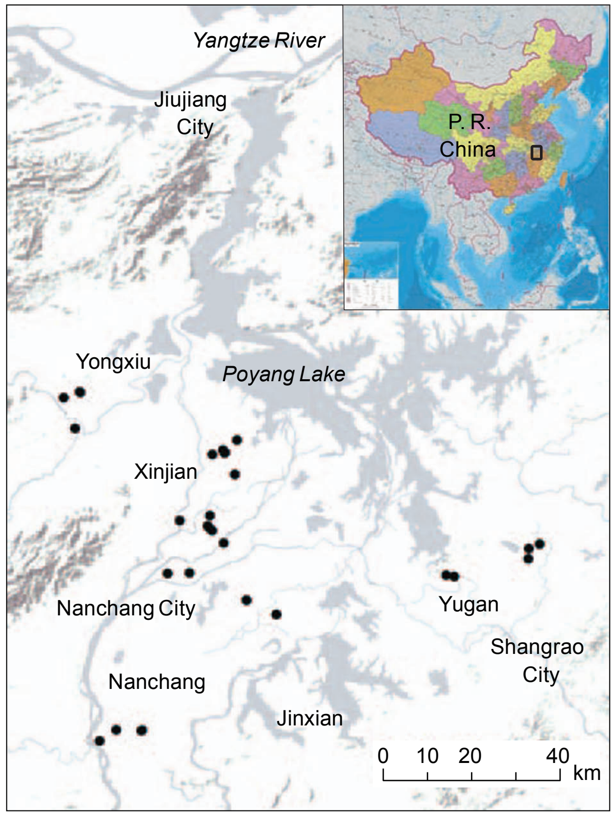

Fig. 1 Study area of domestic duck movements at Poyang Lake, Jiangxi Province, China. Black dots indicate farms where transmitters were deployed.

2.2. Farm and duck selection

We visited duck farming areas in the five counties from 8–18 January, 2015. The criteria for selecting farms were: 1) farms with owners that would cooperate with our study goals, and 2) farms that planned to sell their ducks before Lunar New Year. Because layers go to markets largely based on timing of egg production and not for food for the Lunar New Year, our primary target species were domestic ducks (*Anas platyrhynchos domesticus*; including several local breeds) raised as broilers. Broilers were selected because of their greater likelihood of entering the market chain within the lifespan of transmitters. However, ongoing AI outbreaks in the study area and lower commercial profit for broilers during our study limited the number of cooperating farms with free-ranging broilers. Thus, we also included layers, caged ducks, and other varieties such as muscovy ducks (*Cairina moschata*) and domesticated wild mallards (*Anas platyrhynchos*) (see Appendix). We included several variables including coordinates and size of farms where transmitters were deployed, farming type, poultry species and numbers, expected date of sale, and body mass of marked ducks.

2.3. Transmitter deployment and analysis

Previous reports suggested that broiler production typically peaks during the month of January just prior to the Lunar New Year (Gilbert *et al.* 2007, 2008; Van Kerkhove *et al.* 2009). We conducted our field work from 8 January to 4 February 2015, 2–6 weeks prior to the Lunar New Year (19 February in 2015), because the transmitter battery was expected to last up to 2 months after deployment under an ideal condition. One of our test transmitters lasted for 66 days and produced 194 GPS fixes. We estimated the daily translocation probability as the proportion of the number of translocation events to the total number of telemetry-days (768 days total) and used a Poisson distributions to estimate its 95% confidence interval (CI; Dobson *et al.* 1991).

The GPS-GSM transmitter (Konstanz University, Konstanz, Germany) developed for this study is box shaped (39 mm×25 mm×14 mm) with four harness mounts at the corners and a flexible 45 mm external antenna. Its total mass of 17 g was approximately 0.9% of a ducks' body mass (0.4–1.4%). The GPS-receiver consists of a u-blox CAM-M8 chip antenna module with a hot-start sensitivity of –156 dBm. The data link to the cellular phone networks is provided by a u-blox SARA-U2 UMTS/HSPA/GSM module. We used data-transmission *via* Short Message Service (SMS), and each SMS had six complete GPS data points with date and timestamp, coordinates, height above sea-level, time to fix, satellites detected, battery-voltage, index of measurement, and speed. For control, we use an ATMEL-ATXMEGA-A4U processor and a flash 8 Mbyte data-memory. Coordinates and associated information were collected and stored in the transmitters and transmitted through GSM cellular phone networks to a central station in Germany and from there to Movebank (http://www.movebank.org). We determined commercial trade and local movements of ducks based on transmitted data including sequential changes in spatial locations, required time for the first GPS fix, and voltage changes of batteries over time. The duty cycle was set to take three GPS fixes (Coordinated Universal Time 00:00, 12:00, and 13:00 h; local time 08:00, 20:00, 21:00 h) with one data transmission per day. To power the tag, we used a 240 mAh rechargeable lithium-polymer cell balancing the trade-off between longer lifespan and better concealment. The cost per transmitter unit was about 80 USD.

For harnessing, we used Teflon ribbon (70–100 cm in length, 8.4 mm in width) with two loops for the breast and belly. Transmitters were hidden as much as possible under the dorsal body feathers to minimize chance of human detection. Some transmitters on smaller ducks were visible at a close range, but we expected that marked individuals would be difficult to identify within a large flock (Fig. 2). Even though farmers agreed to participate in our study and transmitters were well concealed on selected ducks, transmitters could be detected and removed when ducks were captured and sold to a trader or customer. To recover transmitters and collect end-user information, we placed a label on each transmitter with local contact information written in Chinese.

Outliers of GPS fixes were filtered out through visual review. To estimate the home range of tracked ducks, we used ArcMet 10.2 in ArcGIS 10.2 (ESRI, Inc., Redlands, CA, USA) for calculating a MCP (minimum convex polygon) home range for each duck, and we excluded ducks that fewer than seven fixes within one week. We used Oriana 4 software (KCS 2011) for analysis of directional data.

2.4. Ethics and repository of tracking data

Procedures for this field research were approved by Institutional Animal Care and Use Committee of the University of Oklahoma (AUS R12-004). Tracking data from this study are publicly accessible in the Movebank Data Repository (www.datarepository.movebank.org under the doi. 10.5441/001/1.38f467s7).

3. Results

3.1. Telemetry overview

We investigated 54 farms with 100-20 000 ducks in five counties of the Poyang Lake region, and we selected 28 farms where owners were supportive of our work and most birds were expected to be sold before the Lunar New Year holiday. The 28 farms selected for our study had similar numbers of poultry (mean±SD: 2 300±3 700, median: 1 500, *n*=28) that were not significantly different (Mann-Whitney

Fig. 2 Global Positioning System-Groupe Spécial Mobile (GPS-GSM) transmitters deployed on upper back of small (left; #4117, 1.8 kg) and large (right; #4156, 2.5 kg) domestic ducks. The white case of the transmitter is not fully covered by contour feathers in the smaller mottled duck, while the transmitter is rarely visible under the feathers of the larger white Peking duck.

U=742.0, P=0.90) from the average number found on farms surveyed in the region (mean±SD: 2 350±3 500 ducks, median: 1 600, n=54). We deployed 40 GPS-GSM transmitters on 24 broilers and 16 layers from the 28 farms (Figs. 1–2, Appendix). One duck was sampled from each of 20 farms, but in eight farms, two to five ducks were chosen to examine variation in movements of individuals from the same farm.

A total of 1 376 GPS fixes from 659 messages were obtained during the period from 8 January to 18 February 2015. Transmitters provided 34.4±23.6 fixes (range: 2–99) and 16.5±7.5 transmissions (range: 1–34) over 19.2±8.5 days (range: 1–35). Voltage of transmitter batteries declined from 1.34 to 1.24 V through the study, and the time until the first GPS fix ranged between 30 and 400 s. Ducks that were kept indoors or inside shelters required a longer time for the first GPS fix resulting in more rapid battery drainage (Fig. 3). Although we placed labels including our contact information on transmitters, none of 40 deployed tags was returned for inspection.

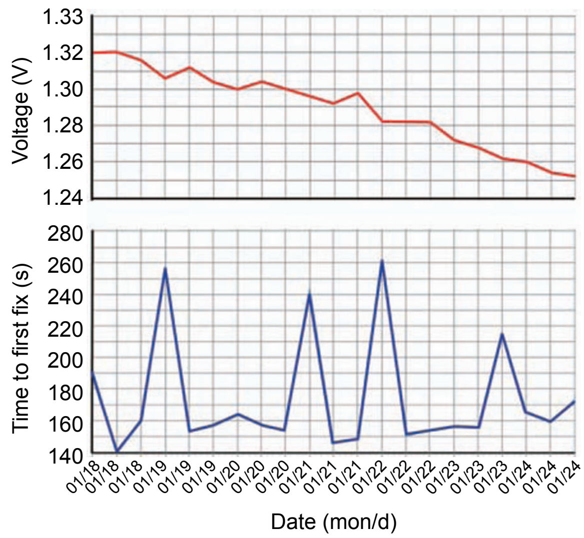

Fig. 3 Example of changes in battery voltage and time taken by the transmitter to acquire the first GPS fix in field tests. This GPS transmitter on a broiler #4117 showed repeated peaks in the time to obtain first coordinates (first fix per set of readings), suggesting that the first or last daily fixes of the free-ranging duck were usually obtained inside its shelter before release in the morning or after it was placed in an enclosure in the evening.

3.2. Market chain

We were able to track the market chain of nine marked ducks transported to other farms, distribution facilities, or markets (Fig. 4, Table 1). Although we expected an increased demand for broilers prior to the Lunar New Year, we found no difference in transportation probability for ducks by market type (6 of 24 or 25% of broilers and 3 of 16 or 19% of layers; Fisher's exact test, P=1.00). Therefore, the daily translocation probability of each duck was estimated to be 1.2% (95% CI: 0.54–2.22).

Layer #4162 and broiler #4175 were transported to wholesale live bird markets in Nanchang and Jingdezhen, while broiler #4171 went to a traditional, local retail market. Broiler #4175 went through a distribution center with 2-day layover (Fig. 4, Table 1). After #4162 was sold to a LBM, the owner replenished his farm with another flock of layers including #4161 which had been raised at one of his other farms.

Three ducks were tracked until they reached distribution center buildings in Jingdezhen (broiler #4170) and Liushui, Zhejiang Province (layer #4188) or to a temporary distribution holding pond (broiler #4152; Fig. 4, Table 1). Broiler #4170 was transported with #4175, but its signal was lost once it reached the distribution facility. Transmission from layer #4188 was lost soon after its arrival to a distribution facility, but broiler #4152 transmitted for 30 days.

The fate and destination of the remaining two ducks was unclear, because the transmitters appeared to have been removed (Fig. 4, Table 1). Broiler #4156 was located on a highway bridge in the northernmost boundary of Jiangxi Province. Although we were unable to retrieve the transmitter, it was abandoned on a typical route to northern provinces (such as Hubei and Anhui provinces), and there were no poultry farms, markets, or end-users nearby. Broiler #4186 was located in shrubs and croplands nearby a residential area where we suspected that it was sold to a family or local retail shop that was located 9 km away from its source farm.

Transport distances ranged from 3 to 396 km (mean±SD: (90.2±125.9) km), and the overall heading for duck movements was non-directional (mean direction: 111.5°, weighted mean direction: 82.9°; Rayleigh's Z=0.374, P=0.70), although eastward movements were more common (Fig. 5). Layer #4188 and broiler #4156 were documented crossing the provincial border, while the other ducks remained within Jiangxi Province.

3.3. Movements of domestic ducks

We also identified four general movement patterns in GPS-tracked domestic ducks: caged ducks, free-ranging ducks returning most nights to a shelter, and area-restricted or unrestricted free-ranging ducks without a shelter (Fig. 6). The average minimum convex polygon (MCP) for the tracked ducks was (177 900±627 800) m^2 (mean±SD; median: 6 500 m^2, n=38) ranging from 270 to 3080 000 m^2 (see Appendix). Except for two unrestricted, free-ranging ducks owned by one farmer that had extensive home ranges of 3 080 000 m^2 (#4189) and 2 450 000 m^2 (#4135), domestic ducks generally moved within restricted areas smaller than 418 200 m^2 (mean±SD: (34 100±83 100) m^2, median: 5 600 m^2, n=36). Free-ranging ducks (mean±SD: (291 400±792

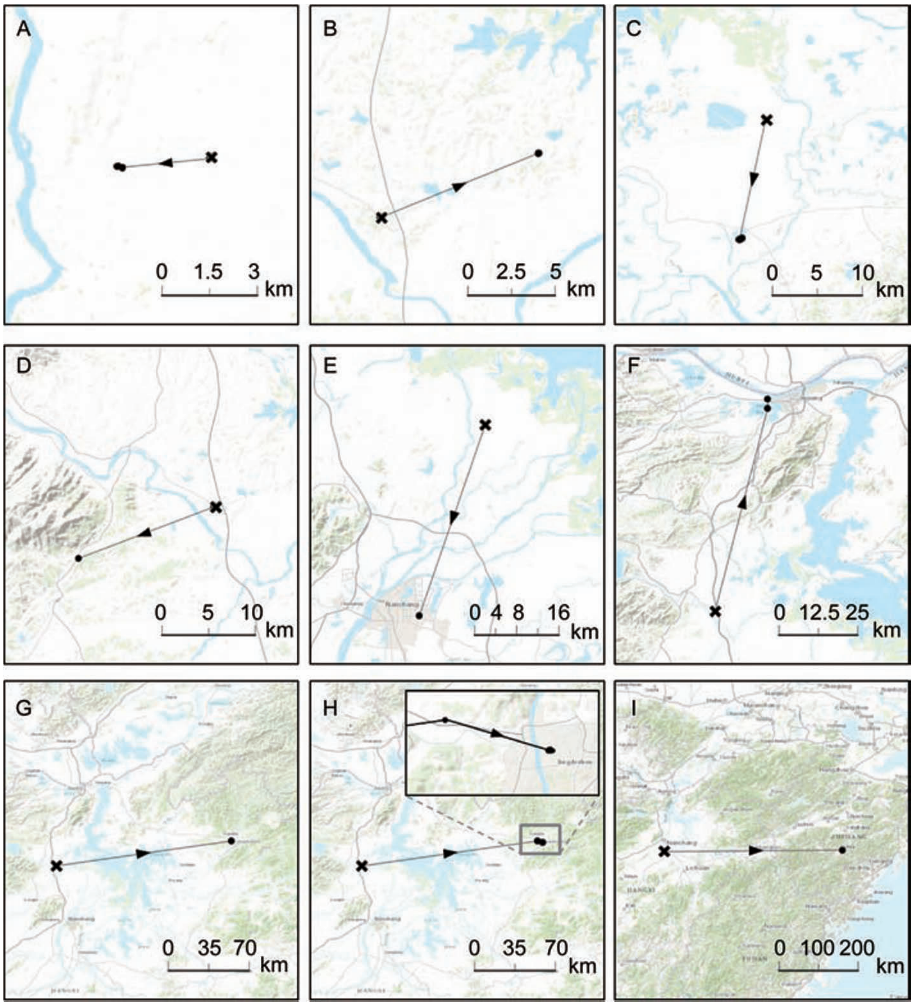

Fig. 4 Movement of GPS-tracked domestic ducks carried from source farms where they were marked (indicated with an ×) to other farms, live bird markets, or distribution facilities (A, #4161; B, #4186; C, #4152; D, #4171; E, #4162; F, #4156; G, #4170; H, #4175; I, #4188). One bird was transported to a live bird market *via* a distribution facility shown in the enlarged area of panel H.

900) m^2; median: 19 300 m^2, n=23) had much larger MCP areas than caged ducks (mean±SD: (3 850±5 050) m^2; median: 2 250 m^2, n=15) (Mann-Whitney U=44.000, P<0.001).

4. Discussion

4.1. GPS-based telemetry for documenting market chains

GPS transmitters have been adopted to identify trade or network of livestock farming by tracking vehicles. In the Republic of Korea, vehicles that regularly visit farms or carry domestic animals and their byproducts (food, waste, beds, and medicine) are required to be equipped and tracked by GPS units under the "Act on the Prevention of Contagious Animal Diseases" as amended on 13 Aug 2013 (Korea Animal Health Integrated System; http://www.kahis.go.kr) after HPAI and foot-and-mouth disease outbreaks. GPS telemetry also has been used to document movement patterns of large livestock to better understand wildlife-livestock interactions and disease transmission (i.e., cattle and wild boar; Barasona *et al.* 2014). However, only recently has miniaturization of this technology enabled us to examine the movements of smaller animals. To our knowledge, this study provides the first demonstration of the ability to obtain a detailed record of movements of marked individuals in a poultry market chain.

We were able to follow nine domestic ducks as they moved along the market chain from Poyang Lake, including movements along a route *via* a distribution facility in a different city. Our study was a successful proof of concept test, but if a larger sample could be deployed, more detailed information could be obtained about market chain differences related to the type and breeds of ducks as well as to characteristics of source farms. Larger farms holding more than 10 000 ducks were less likely to cooperate with

Table 1 Movements of GPS-tracked domestic ducks marked at Poyang Lake, Jiangxi Province, China in January–February 2015

Tag #	Source county	Type	Sex	Mass (kg)	Date deployed	Date moved	Distance (km)	Heading (°)	Destination	Type of destination
4188	Nanchang	Layer	Female	1.8	Jan 23	Feb 5	396	86	Liushui City, Zhejiang Province	Distribution center
4161	Xinjian	Layer	Female	1.7	Jan 16	Jan 18	3	263	Within the source county	Nearby farm (owned by same owner)
4162	Xinjian	Layer	Female	1.7	Jan 16	Jan 17	38	197	Nanchang City	Live bird market
4156	Yongxiu	Broiler	Female	2.5	Jan 11	Jan 13	66	13	Jiujiang City, possibly northern provinces	Unknown — logger removed or lost during transportation
4170	Yongxiu	Broiler	Female	1.7	Jan 12	Jan 17	134	80	Jingdezhen City	Distribution facility
4175	Yongxiu	Broiler	Male	1.9	Jan 16	Jan 17, 20	138	82	Jingdezhen City	Live bird market *via* distribution facility
4171	Yongxiu	Broiler	Male	3.5	Jan 11	Jan 29	14	247	Within the source county	Local retail market
4186	Yongxiu	Broiler	Male	3.9	Jan 17	Jan 19	9	65	Within the source county	Local retail market or end-user
4152	Yugan	Broiler	Male	2.3	Jan 10	Jan 10	14	191	Within the source county	Distribution farm or holding pond

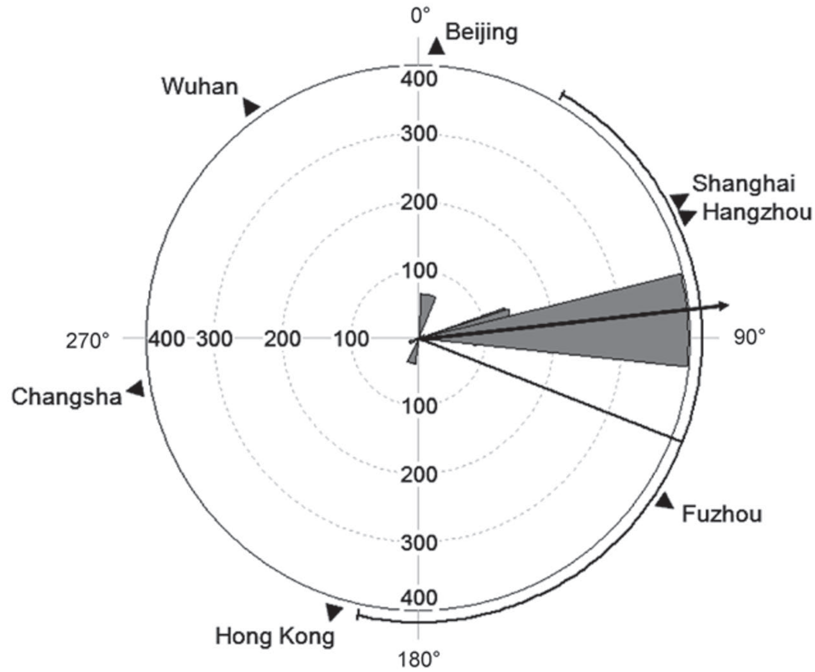

Fig. 5 Rose graph for direction (°) and distance (km) of nine transported domestic ducks with transmitters marked at Poyang Lake, Jiangxi Province, China. The bold line denoted the mean direction of movement and the 95% confidence interval, while the bold arrow indicated the distance-weighted direction. Direction to major cities and capitals of the nearby provinces also were indicated.

our project; thus, our findings may be biased towards market chains linked with small-scale to medium-scale production systems. Nevertheless, live-poultry market networks for the small- to medium-scale systems are important in the spatial epidemiology of avian influenza in Asia (Gilbert *et al.* 2014), and we were able to show that quantitative data could be collected with GPS-GSM transmitters to better understand market chains and their role in HPAI spread.

Our test transmitters were intended to be concealed under the back feathers of domestic ducks, and battery lifespan was expected to last for about two months with three fixes and one transmission per day on the basis of ideal test conditions. Overall performance of the GPS transmitters in the field averaged 29% of the expected lifespan (19.2 of 66 days) and 18% of the expected number of locations (34.4 of 194 fixes). The lifespan of the transmitters may have been affected by several environmental factors (e.g., enclosures, vegetation, temperature) under actual field and farm conditions, but it is likely that the most important cause of rapid battery drainage was increased time for GPS reception and GSM transmission in obstructed situations, since these are the greatest power-consuming processes.

The backpack harness seemed to work well for attaching the transmitters to domestic ducks, as the transmitter seemed well-concealed on the backs of the larger ducks, although transmitters were sometimes visible on smaller individuals (<2 kg). Use of smaller transmitters may improve concealment, but since there is a trade-off between capacity of the battery and miniaturization of the transmitters, adjusting duty cycles may be the easiest method to improve field performance. As we suspected, none of the transmitters were returned to us despite having labels with detailed contact information in Chinese. Thus, it confirmed our contention that GPS loggers that are useful for tracking ducks in rice fields but must be recovered to

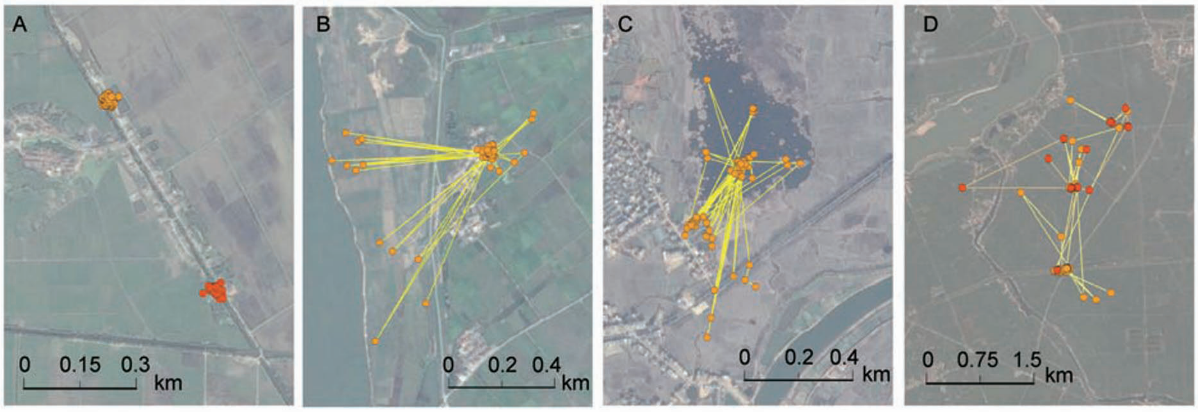

Fig. 6 Four types of local movements of GPS-tracked domestic ducks. A, caged ducks (#4136 and #4155). B, free-ranging ducks returning to a shelter daily (#4187). C, restricted free-ranging ducks without a shelter (#4173). D, unrestricted free-ranging ducks without a shelter (#4135 and #4189).

download their location data (see Prosser *et al.* 2015) are not effective for tracking individuals to document market chains.

4.2. Individual accounts of trade

Our small sample size precluded examining use of this method to compare inter- and intra-farm differences in market chains and to identify the different trades by the different breeds, types, and size of the ducks. However, the direction of movements and distance of duck transportation (3 to 396 km) suggested that domestic ducks raised at Poyang Lake were being widely distributed. It also suggested that frequent HPAI outbreaks at Poyang Lake (Wang *et al.* 2013; Cappelle *et al.* 2014) may result in local and regional spread of infected birds through these market chains. Transportation to eastern markets seemed to be most common, although our analysis was not statistically significant, because longer distance trends were obscured by the many non-directional, local movements. The general eastward direction of movement would correspond to areas that have had the highest LPAI (H7N9) infection risk (Gilbert *et al.* 2014). Thus, directionality should be one of the metrics included in future applications of this technique.

Three layers were transported outside the farms to a live bird market, a distribution facility, and a nearby farm owned by same owner. We tracked movements of #4161 from farm No. 21 to No. 19 for replenishment (Fig. 4-A) one day after the transport of layers from No. 19 (including #4162) to a LBM in Nanchang (Fig. 4-E). Because farm No. 21 was adjacent to muscovy farm No. 20 with broilers #4149 and #4157 that shared the same pond, we determined that three different farms with two duck species were connected through one LBM in Nanchang City. These movements showed two different types of network movements: those from the source farm to market and those between farms. Since farmers commonly buy layers and duck food from LMBs in this region (Wang *et al.* 2013), the production cycle of layers around Poyang Lake was closely linked to the LBM network.

Two free-ranging broilers from farm No. 7 were transported together to a distribution facility 134 km away, and broiler #4175 ended up in a LBM after a 2-day layover in the facility. Broiler #4152 was held in a pond for 30 days, suggesting that not all broilers are slaughtered immediately. The duration of time that ducks remain in the market may influence the spread and persistence of AI viruses over time (Gilbert *et al.* 2014). Distribution facilities may create similar transmission conditions to those of small to medium LBMs and could serve as additional hubs of AI virus exchange between poultry from different farms. The method we tested here should provide critical field information for developing and testing more realistic models of AI transmission risks.

Layer #4162 and broiler #4175 were transported to large LBMs, while broiler #4171 went to a local market. Unfortunately, we were unable to determine if any of our marked ducks reached end-users, and it was difficult to determine the specific fate of the ducks and transmitters in the markets. Live markets seemed to be the final destination of tracked ducks when their transmitters were likely removed; thus, use of transmitters to examine market chains likely will be most useful for examining source-to-market networks rather than to determine movements from markets to their end-users.

4.3. Type of commercial duck productions in Poyang Lake

Understanding poultry production dynamics is important for implementing preventive measures against zoonotic diseases, but the diversity of poultry-producing systems in China have not been fully examined (Wang *et al.* 2013). When we separate commercial production from backyard poultry approaches in China (Wang *et al.* 2013), the farms sampled in this study belong to the smaller-end commercial production system in terms of the farm inventory (100–20 000 ducks).

Not surprisingly, the ducks we marked in cages had very limited movements (around 4 000 m^2) that were restricted by the size of the fenced areas at the source farms. This type of husbandry maintains high duck densities over extended periods with reduced likelihood for interaction of poultry with wild waterfowl compared with ducks in free-ranging farming systems. Free-ranging ducks are released to the fields in the morning and herded back to shelters at dusk, resulting in repeated and regular daily duck movement patterns (see Prosser *et al.* 2015). Free-ranging ducks were distributed in areas 75-times larger than those in fenced areas suggesting higher chances for contact with wild waterfowl.

We recognized that some free-ranging flocks did not return to a specific shelter. These domestic ducks may move freely with minimal human management, overnight in rice paddies or wetlands, and interact with wild waterfowl that are often active at night. Although temporal overlap between wild birds and poultry may not be necessary for AI virus transmission due to virus persistence in natural environments (Domanska-Blicharz *et al.* 2010), temporal as well as spatial overlap of habitat use may result in much higher chances of the introduction of LPAI to poultry and re-introduction of HPAI into wild populations by increasing contact risk between the two groups.

The farming and husbandry types described above may not be always separable due to the diversity of farming practices, variable local landscape features, as well as the large time interval between GPS fixes. However, marking ducks from different farming types may contribute to better understanding of their movements and subsequent roles of each farming type in AI virus reassortment and transmission.

Despite our initial assumption of increased demands for broilers before the Lunar New Year (Gilbert *et al.* 2007, 2008; Van Kerkhove *et al.* 2009), we did not document increasing demand and distance transported over time. The low number of broilers may have been related to decreased profit for broilers at Poyang Lake in recent years and mismatch with the production cycle. Farmers suggested that timing of free-ranging duck production followed the harvest of the rice paddies in October (see Cappelle *et al.* 2014), and ducks arrived in markets before December. That market cycle was earlier than that described in previous work that estimated peak distribution was between January and February (Gilbert *et al.* 2007, 2008). Duck farming cycles may vary depending on production of layers or broilers, among breeds such as mallards and other domestic ducks, and with differences in regional rice cropping cycles. For example, broilers at Poyang Lake are commonly smaller in body size and used for soup in southern China where demand is less related to Lunar New Year than for larger breeds transported to northeast China. Among the 26 domestic duck breeds in China with different sizes and shapes and a wide range of economic and medical usage (Li *et al.* 2010), the pattern of production cycles and distribution may vary widely and greatly affect the complexity of their market chains.

4.4. Cost and benefit of telemetry

In our proof of concept study, we estimated that total telemetry costs were about 4 000 USD including 3 200 USD for 40 transmitters (80 USD per transmitter) and 500 USD for GSM charges (<1 month of data). The success of this type of study is highly dependent on selection of ducks that move immediately into the market chain within a few days of marking, as the cost per successful duck would be greatly reduced if more than 22.5% of the marked individuals provided locations in the market chain.

While data obtained through interviews and questionnaire surveys may provide valuable information about market chains (i.e., Van Kerkhove *et al.* 2009; Soares Magalhães *et al.* 2010; Martin *et al.* 2011b; Fournié *et al.* 2012, 2013), these methods are limited to knowledge of market movements perceived by poultry traders and market authorities. Respondent surveys do not describe how and when individual ducks move from producers to LBMs or to other destinations, while telemetry provides detailed time-specific high-resolution location data including source to market or among network components. Information collected from telemetry will improve development of more realistic HPAI risk models including improved information for social network analysis (Martin *et al.* 2011b) or agent-based models (Kim *et al.* 2010).

5. Conclusion

Developing an approach to examining market chains with telemetry may improve our knowledge of poultry market chains associated with HPAI spread and persistence. Still, there are many issues that need to be considered for successful use of telemetry in market chain studies. Although transmitter deployment may be allowed by farmers at source farms, the live poultry traders, local farmers, and vendors encountering the marked animals in the market chain may remove the transmitters from the ducks at any time during the process. Smaller transmitters may result in better concealment on the marked individuals to minimize detection and removal. Transmitters used in our study lasted 19 days on average, but we predicted a lifespan of up to 2 months.

GPS fixes during transportation were sporadic, probably related to ducks being transported and stored in areas or cages that did not allow for clear transmission of signals.

Thus, balancing increased signal strength with greater capacity batteries while maintaining a transmitter size that is not readily detected is a challenge for future market chain studies that apply this methodology. Programming transmitters to collect coordinates in the early morning and late evening provide locations for ducks in shelters but may increase the time for the first fixes, draining batteries more rapidly as the transmitters search for satellite signals. It may be more efficient to set the duty cycle to collect GPS fixes and transmit to communication towers during mid-day when domestic ducks are commonly outdoors. Other bio-logging sensors such as activity, mortality, or body temperature sensors incorporated in the transmitters could increase our understanding about the fate of the marked ducks and also may indicate their infection status (M. Wikelski, unpublished data).

Our findings provide the first direct information on poultry market network connectivity, albeit for simple and partial market chains. Information and lessons learned from this study demonstrate great potential for future telemetry studies in poultry network analysis by tracing individual hosts with GPS-GSM transmitters. Detailed data from future telemetry studies that apply the techniques tested here will contribute to improvement of HPAI risk assessment models and scenarios with detailed information on poultry market-chain movements.

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Appendix associated with this paper can be available on http://www.ChinaAgriSci.com/V2/En/appendix.htm

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