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Social network analysis of the movement of poultry to and from live bird markets in Bali and Lombok, Indonesia

Abbreviated title: **Analyses of poultry movement networks in Indonesia**

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Summary

Highly pathogenic avian influenza H5N1 has resulted in large losses to the Indonesian poultry sector. Evidence suggests that live bird markets (LBMs) play an important role in the epidemiology of the disease. Knowledge of the frequency and type of contact between the various poultry market players should allow animal health authorities to develop a better understanding of factors influencing virus transmission between Indonesian villages. A questionnaire-based cross-sectional survey was conducted in 17 LBMs on the neighbouring Indonesian islands of Bali and Lombok to investigate the movement patterns of poultry to and from markets. Using social network analyses, a network of contacts was created for each island from a total of 413 live poultry traders and 134 customers. Individual nodes with high degree and/or betweenness were identified in each network. The Lombok network was more dense and connected than the Bali network indicating that disease transmission would be more efficient in the Lombok network. Our findings indicate that whilst live poultry are typically transported over relatively short distances of approximately 10 km, it is not uncommon for traders and customers to travel in excess of 100 km to buy or sell poultry, which may facilitate the spread of disease over a large geographical area. This study highlights the different roles markets play in poultry movement networks and their potential for disease dissemination. The identification of highly influential market nodes allows authorities to target HPAI surveillance activities to locations where disease is more likely to be present, which is crucial in low-resource settings.

Keywords: highly pathogenic avian influenza, H5N1, Indonesia, live bird markets, social network analysis.

Introduction

The emergence of highly pathogenic avian influenza (HPAI) subtype H5N1 in Indonesia in 2003 resulted in large losses to the poultry sector and the highest number of H5N1-related human deaths to date in a single country (Perez et al., 2002). Despite an overall decline in the incidence of HPAI H5N1 in poultry and humans in recent years, Indonesia experienced a sharp increase in the number of reported HPAI H5N1 outbreaks in poultry in 2016. During the first four months of 2016 alone, 148 cases were reported in poultry compared to 123 cases in 2015 (FAO, 2016). The rise in newly emergent AIVs in the Asian region such as H5N6, H5N8 and H7N9 pose an additional threat to both poultry and human health (Hall et al., 2015; Joob and Viroj, 2015; FAO, 2014; Wiwanitkit, 2013).

Indonesians, in common with most nationalities in South East Asia prefer to purchase live poultry, which are largely traded through live bird markets (LBMs), because they are cheaper and the customer can be assured that poultry meat is fresh and free of disease (Patrick et al., 2014). The mixing of different avian species from various sources means that LBMs provide an ideal environment for virus exchange (Morris et al., 2005). Available evidence suggests that LBMs play a crucial role in the epidemiology of avian influenza viruses (AIVs) in countries where live birds are sold to customers (Fournié et al., 2012; Indriani et al., 2010; Ge et al., 2009). A recent study modelled the risk of HPAI H5N1 transmission through poultry movements in Bali concluded that there is a high risk of a LBM being infected despite a low level of disease at the village level (Roche et al., 2014). The limited resources available in Indonesia for market infrastructure and management often results in loosely controlled and regulated markets (Suryadarma et al., 2007) with limited or no biosecurity. This may facilitate the circulation and dissemination of avian influenza viruses through the movement of poultry, poultry products and fomites.

Knowledge of the type and magnitude of contacts between the various poultry market players allows animal health authorities to develop a better understanding of factors influencing virus transmission. To-date, information is limited on the types and frequencies of contacts that exist between live bird markets and poultry traders in Bali and Lombok, and how these contacts might

influence or act as pathogen transmission routes. This information could be useful in identifying villages and markets that are at a greater risk of receiving and dispersing infectious material throughout a network.

In order to establish a network of contacts, information on the movement of poultry between markets and villages is required. This can be achieved by carrying out a survey to document the source and destination village of birds traded in a market, and then analysing the accumulated data using social network analyses (SNA). Social network analyses are concerned with 'relationships' that exist between pairs of individuals in a given study population as opposed to characteristics of the individuals themselves (Borgatti et al., 2009). This perspective recognises that the way in which individuals are connected in a population are important determinants of infection spread (Luke and Harris, 2007).

Although SNA was initially used in the social sciences (Borgatti et al., 2009), it has gained popularity in veterinary epidemiological research. In recent years, network analysis has been used to investigate associations between poultry trade networks and trader practices in Cambodia (Van Kerkhove et al., 2009) poultry trade networks and HPAI H5N1 outbreaks in Vietnam (Soares Magalhães et al., 2010) and China (Martin et al., 2011) and in the identification of high risk players in the backyard poultry industry in Thailand (Poolkhet et al., 2013). Social network analysis is also a useful tool to identify markets that pose a greater threat in terms of disease transmission potential as demonstrated by Fournié et al. (Fournie et al., 2013).

With this background, the aim of this study was to use social network analysis to investigate the movement patterns of poultry to and from live bird markets in Bali and Lombok, and to describe the topology and network of contacts between villages. This will allow for a better understanding of the potential for transmission of disease arising from movement of birds between villages and markets. Information gathered from studies of this type can be used to identify highly connected nodes (i.e. villages and markets) within each network. Based on the biologically plausible assumption that highly connected nodes are more likely to either receive or distribute infection, these locations can then be preferentially targeted for surveillance or enhanced biosecurity measures (Martin, 2006; Christley, 2005).

Materials and methods

A detailed description of the methods used in this study are provided by Kurscheid et al. (2015). The following sections contain a brief overview of the study methods and additional details not published elsewhere.

Study location and respondents

A cross-sectional study of live poultry traders (vendors and collectors) and customers (those purchasing poultry) was carried out between 2008 and 2009 at nine LBMs in Bali (representing approximately 8% of the estimated 109 LBMs) and eight in Lombok (22% of the 36 known LBMs). Markets were selected based on the following criteria: size of the market; approximate volume of poultry traded per day; medium to high flow of road traffic (expected to have a larger customer base) surrounding the market; operating frequency; poultry farm density in the surrounding area; and whether there had been any locally confirmed reports (i.e. confirmed by the Regional Office of Livestock and Animal Health) of HPAI H5N1 outbreaks in poultry in the previous 12 months.

Traders were defined as either a 'vendor' (i.e. retailers) or a 'collector' (poultry wholesalers) depending on their role in the market. Vendors primarily sold live poultry directly to customers at the market, whereas collectors collected live poultry from all sectors of the poultry industry and transported them to the markets either on the same day or a few days later and selling to both LBM vendors and customers (Kurscheid et al. 2015). Customers were defined as individuals purchasing live poultry (i.e. not slaughtered or dressed birds) from vendors or collectors on the day of interview for a variety of purposes (e.g. special cultural or religious events, consumption at home or restaurant and restocking). Study participants were comprised of individuals that were engaged in one of the three aforementioned roles at the market on the day of interview and selected using convenience sampling. The numbers of respondents interviewed at each of the surveyed markets, along with estimates of each group of respondents frequenting the markets on a daily basis, are shown in Tables S3 and S4 of the Supplementary Information. In the remainder of this paper the term 'respondent' is used to refer to individuals interviewed for this study.

Data collection

A semi-structured questionnaire was developed for each of the three categories of respondents in English and translated into Bahasa Indonesia. Questionnaires were administered by face-to-face interviews. Poultry traders were asked to provide details of: (1) the origin of birds being sold, including the type of source (e.g. backyard farm, commercial farm, market or trader); (2) the

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type and number of birds sold on the previous trading day brought to the market for sale; and (3) other markets where birds were sold. Customers were asked to provide details of: (1) the destination of birds purchased on the day of interview; (2) other markets where birds were purchased; and (3) the number of birds purchased on the day of interview.

Data management and analysis

Data from the interviews were entered into a relational database (Microsoft Office Access 2003). The database contained three groups of tables: (1) poultry traders, (2) poultry customers, and (3) village locations. Contacts were defined by the direction of poultry movement, either inbound or outbound, and the village of origin or destination. The interview responses from the database were exported to a social network analysis package (UCINET v6.137 Analytic Technologies Inc., Harvard, Massachusetts, USA).

The names of each of the villages cited by the respondents were cross-matched with digital maps of village and town locations in Bali and Lombok (Anonymous 2014) using the Geographic Information System Quantum GIS (Quantum GIS Development Team 2016) and Google Earth (Google Earth v5.1, Google Inc., Mountain View, USA) to obtain the longitude and latitude coordinates of the village centroid. In the event that coordinates for a village provided by the respondent were not available, those of the nearest village were used. Given that villages of the same name are found in multiple districts throughout each island, the coordinates of duplicate villages closest to the market where interviews took place were used based on interviewer feedback, on the assumption that respondents lived close to the markets where the interviews were taking place.

Descriptive analyses of the data consisted of summary statistics of surveyed participants stratified by direction of movement (to or from a market) and location (source or destination of poultry). Straight-line (Euclidean) distances travelled by respondents transporting live birds to and from markets (in kilometres) were calculated using the latitude and longitude of villages and markets using the fields package in R (Nychka et al., 2015).

The presence of a recorded movement event between locations (i.e. markets and/or villages), and the type of respondent (trader vs. customer) allowed us to construct a network of contacts. Using this approach, markets and villages formed the nodes (vertices) of the network and the presence of a stated movement of live poultry from one node to another formed binary ties. Under the

assumption that transactions between markets and villages were in a specific direction (i.e. from market to village, or village to market), all networks were treated as directed.

Contact networks were constructed for movements relating to the sale or purchase of live poultry. Each network was described in terms of: (1) the number of nodes and directed links; (2) the network size, diameter and density; and (3) the number of reachable pairs of nodes and the proportion of pairs that were reachable. The following parameters were calculated for each node of the network and summarised for the entire network, using frequency histograms and descriptive statistics: in- and out-degree, in- and out-degree centralisation, betweenness and geodesic distance. In addition to absolute measures of node centrality (e.g. in-degree, out-degree and betweenness) normalised centrality measures were calculated as the absolute score divided by the maximum score for the given measure, expressed as a proportion. Normalisation allowed node centrality measures for the two networks (Bali, Lombok) to be compared. Network diagrams were constructed for the two networks. Information regarding the key metrics of social network analysis can be found in the review of Dubé et al. (Dubé et al., 2009). Additional metric definitions are provided in the footnotes of Table 1.

The association between normalised in-and out-degree indices and normalised total degree and normalised betweenness was quantified using Spearman's rho.

Ethics statement

The study protocol was reviewed and approved by the Murdoch University Human Research Ethics Committee, Perth, Western Australia (Permit number 2008/162). Further details are provided by Kurscheid et al. (2015).

Results

Respondents

A total of 413 (Bali $n = 195$, Lombok $n = 218$) traders and 134 (Bali $n = 52$, Lombok $n = 82$) customers participated in this study. Of these, source and destination information was elicited from 95% of respondents from Bali ($n = 184$ traders and $n = 50$ customers) and 90% from Lombok ($n = 196$ traders and $n = 74$ customers). The remaining 43 respondents ($n = 13$ and 30 from Bali and Lombok, respectively) either did not provide information about where birds were transported to and from, or the GPS locations of village names provided were not available. The survey refusal rate was zero.

Network size

The two networks created for the movements of live poultry to and from live bird markets were comprised of 9 markets and 130 villages in Bali (Fig. 1) and 8 markets and 134 villages in Lombok (Fig. 2). Although the number of nodes (i.e. network size) was similar for the two networks (139 for Bali and 142 for Lombok), Lombok recorded more than twice the number of links compared to the Bali network (880 vs 373, Table 1).

Fig. 1 Bali network projected onto geographical map of Bali. Villages and surveyed markets represented by blue and red nodes, respectively.

Fig. 2 Lombok network projected onto map of Lombok. Villages and surveyed markets represented by blue and red nodes, respectively.

Centrality

Degree

Inspection of plots of the cumulative distribution of degree among nodes showed highly skewed degree distributions for both networks with power law function parameters of 2.04 and 2.14 for Bali and Lombok, respectively (see Figures S3 and S4 in the Supplementary Information). The number of incoming movements varied more widely than outgoing, indicated by the higher in- vs. out-degree centralisation values for both networks (Table 1). However, nodes with a null in-degree (i.e. villages that did not receive poultry from any other village) outnumbered those with a null out-degree (i.e. those villages that did not distribute poultry to other markets or villages) for both the Bali ($n = 82$ vs. 26) and Lombok networks ($n = 82$ vs. 25). Hence, the majority of nodes within each network had at least one out-going and no incoming poultry movements and only a few had a large number of incoming movements compared with outgoing movements.

The maximum number of incoming movements recorded for a single node was 2.4 times greater for Lombok than for Bali ($n = 125$ vs. 52). The Lombok network also showed greater variation in incoming movements compared to the Bali network, as indicated by the higher normalised values for the mean (0.04 vs. 0.02, respectively) and range of in-degree scores (0 – 0.89 vs. 0 – 0.38). Normalised out-degree centralisation values and the range of out-degree scores showed a similar pattern (Table 1). Although the numbers of incoming and outgoing movement events were greater among markets in Lombok, the proportions of movements to and from unique contacts were higher in Bali (Supplementary Information). Another difference between the two

networks in terms of degree was that for Lombok, non-surveyed villages had high degree scores as well as the surveyed markets. In Bali, on the other hand, only the surveyed markets had high degree scores. The number of movements recorded for non-surveyed nodes in the Bali network were relatively small in comparison with inbound movements ranging between one and four and outbound between one and ten.

Normalised values for in- and out-degree were plotted against each other for the two networks (Fig. 3) to determine if villages and markets that had a high number of incoming poultry movement events also had a high number of outgoing poultry movement events. Plots for each network indicated that a correlation was present. To evaluate this further in- and out-degree indices for all nodes were analysed using the Spearman's rho test. The resultant R-values showed that a statistically significant correlation between normalised in-degree and out-degree was present for Lombok ($R = 0.31$, $p < 0.001$) but not for Bali ($R = -0.10$, $p = 0.241$). However, a statistically significant positive correlation was identified between in- and out-degree among the surveyed market nodes in the Bali network ($R = 0.69$, $p = 0.040$) but not among the surveyed market nodes in the Lombok network ($R = 0.65$, $P > 0.05$).

Table 1. Summary statistics for the Bali and Lombok networks

Parameter ^a	Bali network	Lombok network
Network size		
Number of nodes	139	142
Number of directed links	373	880
Size	19182	20022
Diameter	6	8
Measures of centrality		
Mean in-degree (range)	2.68 (0 - 52)	6.20 (0 - 125)
Mean out-degree (range)	2.68 (0 - 33)	6.20 (0 - 61)
Normalised mean in-degree (range)	0.02 (0 - 0.38)	0.04 (0 - 0.89)
Normalised mean out-degree (range)	0.02 (0 - 0.24)	0.04 (0 - 0.43)
In-degree centralisation	0.36	0.84
Out-degree centralisation	0.22	0.39
Mean betweenness (range)	25.46 (0-651)	111.50 (0 - 3259)
Normalised mean betweenness (range)	0.00 (0-0.03)	0.01 (0 - 0.17)
Betweenness centralisation	0.03	0.16
Measures of cohesion		
Density (directed)	0.02	0.04
Mean geodesic distance (mode)	3.79 (4)	2.69 (3)

Number of reachable pairs	2292	8035
Proportion of reachable pairs	10.9%	40.0%
Clustering coefficient ^b	0.16	0.40
Distance-based cohesion (or compactness) ^c	0.04	0.16
Distance-weighted fragmentation ^d	0.96	0.84

^a See Dubé et al. (2009) for definitions of network parameters.

^b Calculated on undirected networks.

^c Compactness is the normalized sum of the reciprocal of all the distances (i.e. based on the lengths of paths). This has a value of 1 when the network is a clique (everyone is adjacent) and zero when the network is entirely made up of isolates.

^d Distance-weighted fragmentation is 1 minus compactness and describes the breadth of the network (Borgatti, 2006).

Fig. 3 Scatterplot of normalised out-degree as a function of normalised in-degree for the Bali and Lombok networks.

Betweenness

Although the normalised mean betweenness scores for both networks were similar (0.00 vs. 0.01, for Bali and Lombok, respectively) both the maximum betweenness value and betweenness centralisation indices for the Lombok network were five times greater than for the Bali network (Table 1). Scatterplots of normalised betweenness as a function of total degree (Fig. 4) showed a positive correlation between the two measures for both networks. This was further demonstrated using the Spearman's Rho test, producing R-values of 0.54 ($p < 0.001$) and 0.73 ($p < 0.001$) for Bali and Lombok, respectively. A statistically significant association between degree and betweenness for markets was identified in the Lombok network ($R = 0.87$, $p = 0.004$) but not in the Bali network ($R = 0.48$, $p > 0.05$).

Fig. 4 Scatterplot of normalised betweenness as a function of normalised total degree for the Bali and Lombok networks.

Network cohesion and topological features

The density (i.e. the proportion of potential contacts in a network that were actually present) for both networks was low (2% for Bali and 4% for Lombok) which is not surprising because the data were collected from a subset of LBMs in each island. Although the cohesion (i.e. compactness) score for the Lombok network was four times higher than the Bali network (0.04 vs. 0.16), both values were relatively low. Both networks had similar, relatively high

fragmentation scores (0.84 and 0.96 for Lombok and Bali, respectively). The total number of reachable pairs of nodes within the Lombok network was 8035 representing 40% of all possible pairs, which was 3.5 times as many as in the Bali network (2292, 11%). Furthermore, the average number of nodes that could reach other nodes was 56.8 in the Lombok network compared with 15.4 in the Bali network. The proportion of nodes that had zero reachability (i.e. had no outgoing poultry movements and therefore could not reach any other node) was similar for Bali (19%, $n = 26$) and Lombok (18%, $n = 25$).

Geodesic distances between pairs of reachable nodes varied more widely in the Bali network (Fig. 5) resulting in a larger mean geodesic distance of 3.79 compared to 2.69 for the Lombok network. Mode values for geodesic distance indicated that most nodes within the Lombok network could be reached within three 'jumps' compared to four in the Bali network. The clustering coefficient for the Bali network was relatively small compared with the Lombok network (0.16 vs. 0.40). A random (directed) network of similar size to the Bali network produced a mean geodesic distance of 4.8 and a clustering coefficient of 0.02. The mean geodesic distance and clustering coefficient for a random (directed) network of similar size to the Lombok network was 3.0 and 0.04, respectively.

Fig. 5 Frequency histogram of geodesic distances for the Bali and Lombok networks.

Movement distances

Respondents in Bali transported poultry over slightly shorter distances (median = 5.3 km, IQR: 2.3-12 km) than Lombok (median 8.6 km, IQR: 4.6-16 km). However, the range of distances was similar for the two islands (0-111 km and 0-122 km, respectively), with the greatest distance in Lombok occurring between two villages as opposed to between a market and village in Bali. Comparison of distances travelled by respondent categories showed little differences between vendors (median = 7.3 km, IQR: 4.2-15 km) and collectors (median = 9.8 km, IQR: 5.5-16 km). Traders, in general, transported birds over greater distances compared to customers (median = 4.4 km, IQR: 1.8-10 km). The average movement distances of each respondent type differed significantly in Lombok ($F_{2,877} = 7.90$, $p < .001$) but not in Bali ($F_{2,370} = 1.08$, $p > 0.05$). *Post-hoc* analysis of average distances travelled by respondents in Lombok identified significant differences between vendors and customers ($p = 0.003$) and collectors and customers ($p < 0.001$) but not between vendors and collectors ($p > 0.05$).

Village-to-market (median 7.7 km, IQR: 3.2-13 km) and market-to-village movement distances (median 7.7 km, IQR: 4.6-14 km) in Lombok were almost identical however the maximum distance travelled in Lombok was greater for market-to-village movements (105 km vs. 66 km). In contrast, maximum distances travelled in either direction in Bali were the same (112 km), whilst village-to-market distances (median = 5.3 km, IQR: 2.6-12 km) were slightly greater than market-to-village movement distances (median = 3.5 km, IQR: 0.0-3.9 km). Box and whisker plots of market-to-village and village-to-market movement distances for each of the surveyed markets and for the three different respondent types are provided in the Supplementary Information (Figures S5 to S12).

Off-island movements were recorded for both Bali and Lombok. One movement event was recorded between a small island (Nusa Penida) off the south-east coast of Bali and the surveyed market Galiran. In Lombok, a single collector reported transporting birds between Lombok and Sumbawa islands but did not involve direct movements to or from any of the surveyed markets.

Discussion

Live bird markets facilitate the movement of poultry through extensive networks that can span large geographical areas (Soares Magalhães et al., 2010). Therefore, understanding trade patterns and animal movements within live poultry marketing industries provides essential knowledge concerning the likelihood of disease transmission by contact. Currently, this information remains limited in Bali and Lombok and many other parts of Indonesia. The aim of this study was to investigate the movement of live birds to and from selected live bird markets, which represented the main types of markets found in Bali and Lombok, in order to identify the type and magnitude of contacts that exist between live bird markets, poultry traders and poultry customers. From the data collected in this cross-sectional study, two networks of contacts were constructed from which descriptive analyses were carried out, enabling the identification of important characteristics pertaining to network topology and key nodes within each network (Kiss et al., 2006).

Findings from this study showed that whilst most respondents transported birds to and from markets over distances of approximately 10 km, there were also traders and customers who travelled much larger distances (in excess of 100 km) to buy or sell poultry. A study of poultry trade networks in Cambodia found that middlemen (i.e. collectors) travelled further in pursuit of collecting and trading poultry than retailers (i.e. vendors), who rarely sold poultry outside of their home village (Van Kerkhove et al., 2009). This study found that traders typically travelled

greater distances than customers. The reasons why some traders and customers travelled large distances to buy or sell poultry were not ascertained in this study. It is reasonable to assume that traders may travel large distances to source poultry from specific locations (whether it be a farm, market or other traders) or sell poultry where they know the demand is expected to be higher. Explanations for the large distances travelled by some customers is however unclear. It could be speculated that customers purchase poultry from a market close to their home for a family celebration or religious ceremony that may be taking place in a distant location. Other factors that may influence this behaviour are the availability or price of specific bird types. In traditional Hindu culture (of Bali), different types of chickens and ducks (i.e. specific colours or physical characteristics) are often required for different ceremonies (Mastika, 2007).

The identification of nodes with the most central positions in the network allows resources to be specifically targeted towards those nodes for disease control programs, which is particularly important in low-resource settings (Van Kerkhove et al., 2009). Degree centralisation indices provide a measure of the number of incoming and outgoing movements for each node. Higher values represent nodes with larger numbers of ties and these are therefore more likely to have a greater influence in the network (May and Lloyd, 2001). In-degree can be thought of as a measure of 'receptivity' or 'popularity' whilst out-degree measures 'expansiveness' (Wasserman, 1994). In terms of disease transmission, nodes with high in-degree scores are more likely to become infected due to the higher number of potentially infected birds entering the node. High in-degree nodes may also be important 'disease spreaders' if they also have high out-degree scores (Kiss et al., 2006). Therefore, it is important to identify nodes which have both high in- and out-degree as these have the potential to act as 'super-spreaders' (Shen, 2004).

Both networks presented in this study had greater values for in- versus out-degree centralisation and had more nodes with no incoming movements compared to outgoing movements. It is important to note that these two findings are most likely the result of the disproportionate number of traders (vendors and collectors) interviewed in this study, compared with customers and therefore a greater proportion of nodes represent sources of poultry (i.e. outgoing or village-to-market movements) rather than destinations (incoming or market-to-village movements). Similarly, surveyed market nodes were expected to have higher degree (particularly in-degree) than non-surveyed nodes due to the egocentric data collection approach employed in this study that focused on markets.

Comparison of the two networks identified greater in- and out-degree centralisation indices for the Lombok network compared to the Bali network. This finding is consistent with the highly mobile nature of Lombok's poultry traders, who often source small numbers of birds from several locations compared to Bali where traders generally source larger volumes from smaller numbers of locations (Kurscheid et al, unpublished data). This finding indicates that high degree nodes in the Lombok network play are likely to play a more dominant role in terms of disease transmission compared to those in the Bali network. High degree nodes in both networks would make ideal candidates for disease control programs (Albert et al., 2000), such as increased surveillance (in terms of sampling and bird health checks), enhanced biosecurity measures (e.g. bird zoning and daily cleaning of markets and cages) and education campaigns to increase poultry traders' knowledge and awareness of HPAI and good biosecurity practices.

The importance of high-degree nodes within a network, in terms of disease dissemination, is easily understood because, logically, individuals with a large number of contacts have the potential to spread infection to a larger number of individuals (Bansal et al., 2007). However, the extent of transmission through the entire network depends on the connectivity of the group to which the individual belongs (Stark et al., 2006). Enhanced connectivity (cohesion) facilitates disease dissemination throughout a network whereas fragmentation impedes it (Albert et al., 2000). Despite the fact that details of live poultry movements were elicited from similar proportions of respondents from each island and a similar number of nodes were present within each network, the Lombok network contained 2.4 times as many directed links compared to the Bali network demonstrating that the Lombok network is more connected than the Bali network. Evidence for this was also provided by a number of other observed factors such as a larger cohesion score, smaller values for fragmentation and average geodesic distance and a substantially larger number and proportion of reachable pairs within the network. Therefore, it appears that virus transmission would be more efficient in the Lombok network. The smaller diameter of the Bali network indicates that fewer steps are required for the possibility of a disease to reach any other node in the network compared to Lombok.

Betweenness indices reflect the influence an individual node has within a network. This centrality measure represents the frequency with which a node falls between the shortest path of other nodes and therefore indicates the amount of flow within the network that is controlled by a particular node (Newman, 2003). High betweenness means that a particular node acts as a bridge connecting otherwise unconnected nodes or groups (Wasserman, 1994). This is important in terms of disease control because such nodes provide the bridge over which infection might travel

from one section of a network to another (Dubé et al., 2009). The fact that the normalised betweenness centralisation index of Lombok was more than five times the value of Bali means that a node in the Lombok network falls in the shortest path between two other nodes, on average, five times more frequently than a node in the Bali network. It also indicates that bridge nodes in the network play a greater role in controlling the flow of poultry through the Lombok network compared to Bali. Furthermore, the Lombok network was the only one of the two that was found to have a node with high total degree and betweenness (Figure 4). This node (Narmada market) plays a key role in the network due to the large number of movements to and from the market and its role as a bridge in the network. Furthermore, 40% of the 177 movements recorded for the node were to and from unique contacts, meaning that it has a greater potential to disseminate infection throughout the network than any other node within the Lombok network. Despite this, the removal of this node (i.e. by closing down the market temporarily in the event of an outbreak) would have little impact on the integrity of the network due to its high connectivity. By way of contrast, removal of the node with the largest betweenness score in the Bali network (Galiran market) would cause the main component of the network to fragment into two sub-groups. Removal of one or, incidentally, both nodes with the highest degree would still allow the integrity of the network to remain intact. Therefore, in the event of a reported outbreak in Bali, closure of the market with the largest betweenness score would more likely limit the ability of the virus to diffuse throughout the network compared to closure of other markets. Although targeting the node whose removal partially collapses the network would be a priority in an outbreak response scenario, all preventative, surveillance or control programs should also include the two other highly connected nodes due to their influence and ability to disseminate disease throughout the network (Shen, 2004). The absence of high degree and betweenness nodes in the Bali network suggests that the roles of nodes within this network are quite distinct. In summary, the higher degree and betweenness displayed by the Lombok network indicates a network characterised by 'hubs' and 'bridges' whereas the Bali network is dominated more by hubs alone.

Investigating the topological properties of a network allows us to identify whether the network has random, small world or regular lattice properties (Dubé et al., 2009). Epidemic simulations on theoretical networks have shown how the outcome of an epidemic in terms of size, speed and pattern of diffusion may vary according to the topology of the network (Kiss et al., 2006; Rushton et al., 2005). Whilst many real world networks typically display small world properties, which are characterised by short geodesic distances and high clustering coefficients compared to random networks of similar size (Telesford et al., 2011), neither of the networks in this study

showed these characteristics. However, both networks displayed right-skewed degree distributions meaning that the majority of nodes have low degree whilst a small number, also known as ‘hubs’, have high degree (Dezso and Barabási, 2002). Networks with right-skewed degree distributions are important epidemiologically in terms of dissemination of disease and for surveillance and control programs, largely because they tend to behave in a predictable manner (Barabási and Bonabeau, 2003). Such networks are largely resistant to random control measures because the vast majority of nodes have only a few links and their ‘removal’ has little impact on the network (Albert et al., 2000). Therefore, there is a high probability that selected nodes will have a low degree, causing only slight effects on the rest of the network, and hence, can tolerate random ‘failures’ (or removal) of many nodes before they fragment (Barabási and Bonabeau, 2003). Networks with right-skewed degree distributions are highly susceptible to targeted disease control programs because they rely on relatively few, highly connected hubs to maintain connectivity (Albert et al., 2000). The presence of these highly connected or ‘bridging’ nodes also makes the networks important for the propagation of epidemics as they can transmit disease to many other nodes (Barabási and Bonabeau, 2003). Obviously the more ‘cohesive’ or ‘connected’ a network is, the larger the potential for epidemic spread. Interventions to disrupt spread are different. Random networks are moderately susceptible to targeted efforts or ‘attacks’ and there is little difference between random failures and targeted attacks in random networks (Barabási and Bonabeau, 2003). Hence, targeted control strategies focusing on hubs within the network can be very effective (Dezso and Barabási, 2002).

The availability of resources to investigate outbreaks and to control and prevent further outbreaks is often limited in less-developed and developing countries, such as Indonesia. By utilising knowledge of network characteristics, resources and investigational efforts can be targeted toward markets and villages in central and influential positions within the network (Van Kerkhove et al., 2009).

Currently, there are no formal documentation requirements in place to track movements of poultry traders marketing birds through live bird markets in Indonesia. Therefore, in the event of an outbreak authorities have limited information to direct them to other key markets and villages, which may need to be notified or included as part of control activities. However, with knowledge derived from a poultry movement network analysis similar to that described in this study, markets connected to these villages can be closed and poultry farms and collector yards within these areas can be notified and dealt with accordingly. Knowledge of potentially high risk

markets and villages will also allow authorities to target these for biosecurity improvements and campaigns to raise awareness on good biosecurity practices.

Complete enumeration of contacts is normally required to create an entire network (Bansal et al., 2007), however, given the large number of LBMs operating in Bali and Lombok it was not feasible to conduct a census of all known markets as part of this study. Unfortunately this is likely to have resulted in selection bias and the effects of this bias on the validity of network statistical measures are difficult to quantify (Lockhart et al., 2010; Borgatti et al., 2006; Costenbader and Valente, 2003). It is likely that inclusion of a greater proportion of contacts would alter the connectedness of each network generated. The addition of new nodes may also alter the centrality and consequently the roles that individual nodes played within each network. However, it would be reasonable to assume that the type and level of bias would be similar across both of the analysed networks (Lockhart et al., 2010). Therefore, appropriate inferences can be drawn from this study by focussing on how the parameters for each network vary in relative, rather than absolute terms. Previous studies have shown that there is little difference to the robustness of centrality measures in the event of incomplete data due to either random measurement error and missing data or deliberate sampling on nodes or edges, and that it is reasonable to compute centrality indices when aware of these errors (Borgatti et al., 2006; Costenbader and Valente, 2003; Marsden, 1993). Furthermore, market selection criteria specifically aimed to ensure that key markets covering a broad range of districts in each island were included, thereby increasing the potential scope of contacts, in an effort to capture as much of the complete live poultry movement networks as possible in Bali and Lombok. Another important point to note is that for the current study the number of movements to and from a node (i.e. degree) was derived from survey respondents that provided details of source and destination of birds. Given that a relatively small proportion of respondents did not provide this information and that in some cases GPS locations of village names were not available and were therefore not included in the analyses, it is likely that the calculated degree scores for each market slightly under-represent the true number of movement events occurring to and from each site. The out-degree, in particular, would likely be under-represented given the limited number of customers interviewed for this study compared to traders. This was due to the focus of the study, which primarily investigated the practices and behaviours of live poultry traders working in poultry markets.

The marketing systems in Bali and Lombok rely heavily on the sale of live poultry through markets and each step of the marketing chain involves a number of different players. Prior to

entering the markets, poultry may have changed ownership numerous times and if we associate each exchange with a movement event, this amounts to a large number of movement events on any given market day. Furthermore, findings from other studies (Soares Magalhães et al., 2010; Van Kerkhove et al., 2009) indicate that festivals, religious celebrations and other special events can result in a substantial increase in the magnitude of bird volume and trading frequency occurring with a network. With such large numbers of birds and movement events occurring on a daily basis through the highly complex networks identified in this study, it is not difficult to envision the challenges faced by local authorities in HPAI related activities. Therefore, identifying highly influential nodes within each network allows authorities to target HPAI related activities to where they have better chance of success.

Throughout this study we refer to movements of 'live' poultry. It is important to point out that not all bird movements occurring from markets are of live birds, as customers may have the birds slaughtered prior to leaving the market. Although we did not specifically ask customers whether they intended to have the birds slaughtered prior to leaving, we made the assumption that the majority of birds purchased by customers leave the market alive. This assumption was based on several findings from the survey: (1) only five of the 17 markets surveyed offered slaughtering services in the market (all five of these markets were in Lombok); (2) only two of 134 customers interviewed reported purchasing slaughtered poultry during their visit to the market; and (3) most (64%) customers slaughter their own birds (either at the home or at a slaughter house).

Using the same study design and method for sampling vendors, collector and customers on Bali and Lombok, we identified marked differences in the characteristics the networks generated for each island. Further, we identified specific markets on each island that were likely to be highly influential in the spread of disease (and therefore markets that should be targeted for surveillance or enhanced biosecurity measures). Cross-sectional vendor-collector-customer studies, similar to the study described in this paper, are required to identify LBMs with similar properties in other areas of Indonesia.

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Author contributions

Conceived and designed the study: JK, MS, SF and JT. Developed the questionnaire: JK, MA, IA, SF and JT. Conducted the interviews: MA and IA. Analysed the data: JK, MS, PD and SK. Drafted the manuscript: JK. Revised the manuscript: JK, MS, PD, SF, JT and SK.

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Supporting Information

- Figure S1. Names and locations of each of the $n = 9$ surveyed markets in Bali.
- Figure S2. Names and locations of each of the $n = 8$ surveyed markets in Lombok.
- Table S1. Movements occurring to and from each of the nine surveyed markets in Bali.
- Table S2. Movements occurring to and from each of the eight surveyed markets in Lombok.
- Table S3. Total number of respondents interviewed at each surveyed market in Bali and the estimated number of each group of respondents frequenting each market on a typical day.
- Table S4. Total number of respondents interviewed at each surveyed market in Lombok and the estimated number of each group of respondents frequenting each market on a typical day.
- Figure S3. Cumulative degree distributions for the Bali network.
- Figure S4. Cumulative degree distributions for the Lombok network.
- Figure S5. Box and whisker plot of market-to-village distances travelled in Lombok.
- Figure S6. Box and whisker plot of village-to-market distances travelled in Lombok.
- Figure S7. Box and whisker plot of market-to-village distances travelled in Bali.
- Figure S8. Box and whisker plot of village-to-market distances travelled in Bali.
- Figure S9. Box and whisker plot of market-to-village distances travelled by each respondent type in Lombok.
- Figure S10. Box and whisker plot of village-to-market distances travelled by each respondent type in Lombok.
- Figure S11. Box and whisker plot of market-to-village distances travelled by each respondent type in Bali.

726 Figure S12. Box and whisker plot of village-to-market distances travelled by each respondent
727 type in Bali.

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