Science of the Total Environment

Bats and Nipah virus: long-term market surveys for live bats in trade in southwestern Indonesia

--Manuscript Draft--

Manuscript Number:	
Article Type:	Research Paper
Keywords:	Chiroptera; Indonesia; paramyxovirus; wildlife trade; zoonotic diseases
Corresponding Author:	Vincent Nijman, PhD Oxford Brookes University UNITED KINGDOM OF GREAT BRITAIN AND NORTHERN IRELAND
First Author:	Vincent Nijman, PhD
Order of Authors:	Vincent Nijman, PhD
	Erly Sintya
	Desak Ketut Tristiana Sukmadewi
	Kuntayuni Kuntayuni
	Sukmasari Triana Gita Putri
	Jessica Chavez
	Abdullah Abdullah
	Megan Halbrook
	Ryan J. Harringan
	Sydney Merritt
	Nicole A. Hoff
	Anne W. Rimoin
	Lisa Hensley
Abstract:	Bats are important hosts for many zoonotic viruses, including Nipah virus, a bat-borne emerging zoonotic disease. In southwestern Indonesia, bats are sold at marketplaces for traditional Asian medicines, especially as a treatment for asthma. After purchase bats are slaughtered at the market location where they were sold. These markets present a significant risk for Nipah transmission between bats and humans or bats and intermediate species. Between 2012 and 2025 we conducted 348 surveys in 29 animal markets and counted live bats offered for sale. We recorded 2,238 Pteropus bats and 1,005 Cynopterus bats during 290 (83%) of the surveys, and most markets displayed between 5 and 10 bats, up to 50 bats, at any given time. More bats were displayed on weekends than on weekdays, and over the 14 years covered by our survey trade was stable. There was no observed seasonality in the number of bats for sale. Average asking prices were US$22.25(±1.15) for Pteropus bats and US$12.75±4.19 for Cynopterus bats. Cities where people had lower purchasing power offered more bats per million people than their more affluent counterparts. Indonesia is the largest Muslim country globally by population, and bats are considered haram (unfit for consumption). Consequently, we observed a more bats in regions with larger Christian populations. With thousands of people visiting these markets daily, potentially in close contact with bats, we provide evidence that the live bat trade increases the risk of zoonotic disease spillover, not only for Nipah virus but also other emerging zoonotic diseases.

Powered by Editorial Manager® and ProduXion Manager® from Aries Systems Corporation

Oxford, 23 November 2025

Dear editor

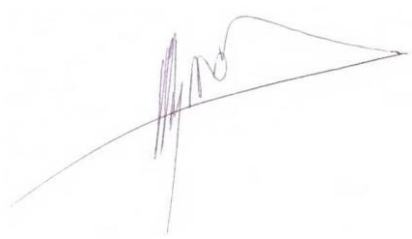
We hereby submit a full research paper entitled “Bats and Nipah virus: long-term market surveys for live bats in trade in southwestern Indonesia” to Science of the Total Environment. Nipah virus a bat-borne emerging zoonotic paramyxovirus (discovered in 1998) with a high case fatality rate in humans (up to 95%). There are no therapeutics to mitigate or cure the disease and no preventative vaccines are available. Nipah virus outbreaks in humans have been recorded in several South and Southeast Asian countries, including Malaysia (first cases), Singapore, and the Philippines, but intriguingly, even though it borders these three countries, it has not been detected in Indonesia. One off surveys of bats for sale in animal markets in west Indonesia has, however, detected anti-Nipah virus antibodies in these in bats.

We surveyed 29 animal markets in southwestern Indonesia, for a total of 348 times, over a 14-year period, during which we detected some 3,500 live bats for sale. We found limited changes over time and higher numbers of bats were offered over the weekend. Indonesia has the world’s largest Muslim population and the consumption of bats for food is considered haram (the interpretation of its consumption for medicine varies); in cities with a proportional larger Christian population, we found more bats for sale. We show the interconnections between human behaviour, trade in wildlife and spillover risks of emerging infectious diseases, and we discuss our findings in the context of a One Health approach. With trade in live bats being prevalent in other parts of the world the lessons learned from Indonesia have wider global implications.

Ours is a truly interdisciplinary study (the authors include an anthropologist, geographer, ecologists, epidemiologists and experts on emerging zoonotic diseases; from the UK, USA and Indonesia), and has a broad relevance and potential global impact. The paper has not been submitted to another journal.

We look forward in hearing back from you

Sincerely yours



Vincent Nijman (on behalf of all the co-authors)

Title page

Title: Bats and Nipah virus: long-term market surveys for live bats in trade in southwestern Indonesia

Authors and affiliations: Vincent Nijman[1,2], Erly Sintya[3,4,5], Desak Ketut Tristiana Sukmadewi[6], Kuntayuni [3], Sukmasari Triana Gita Putri[6], Jessica Chavez[1,2,7], Abdullah Abdullah[8], Megan Halbrook[9], Ryan J. Harringan[10], Sydney Merritt[9], Nicole A. Hoff[9], Anne W. Rimoin[9], Lisa Hensley[11]

1 Oxford Wildlife Trade Research Group, School of Law and Social Sciences, Oxford Brookes University, Oxford OX3 0BP, UK

2. EcoVerde Global Consultancy, Sacramento, USA

3. Center for Climate Change, Warmadewa University, Denpasar 80239, Bali, Indonesia

4. Faculty of Medicine and Health Sciences, Warmadewa University, Denpasar 80239, Bali, Indonesia

5. School of Chemical, Materials and Biological Engineering, Sheffield University, S1 4LZ, UK

6. Management Department, Faculty of Economics and Business, Warmadewa University, Denpasar 80239, Bali, Indonesia

7. School of Biological and Medical Sciences, Oxford Brookes University, Oxford, UK

8. Department of Biology, Universitas Syiah Kuala, Banda Aceh, Indonesia

9. Department of Epidemiology, University of California, Los Angeles (UCLA), Los Angeles, USA

10. Center for Tropical Research, Institute of the Environment and Sustainability, University of California, Los Angeles (UCLA), Los Angeles, USA

11. Zoonotic and Emerging Diseases Research Unit, United States Department of Agriculture Agricultural Research Service, United States Department of Agriculture, Manhattan, USA

Corresponding author: Vincent Nijman, Email: vnijman@brookes.ac.uk

ORCID

Vincent Nijman 0000-0002-5600-4276

Erly Sintya 0000-0002-4081-547X

Desak Ketut Tristiana Sukmadewi 0000-0002-2160-1011

Kuntayuni 0009-0008-2616-9353

Jessica Chavez 0009-0008-9802-5340

Abdullah Abdullah 0000-0003-0046-0333

Megan Halbrook: 0000-0002-3892-2655

Ryan J Harrigan: 0000-0002-4504-7158

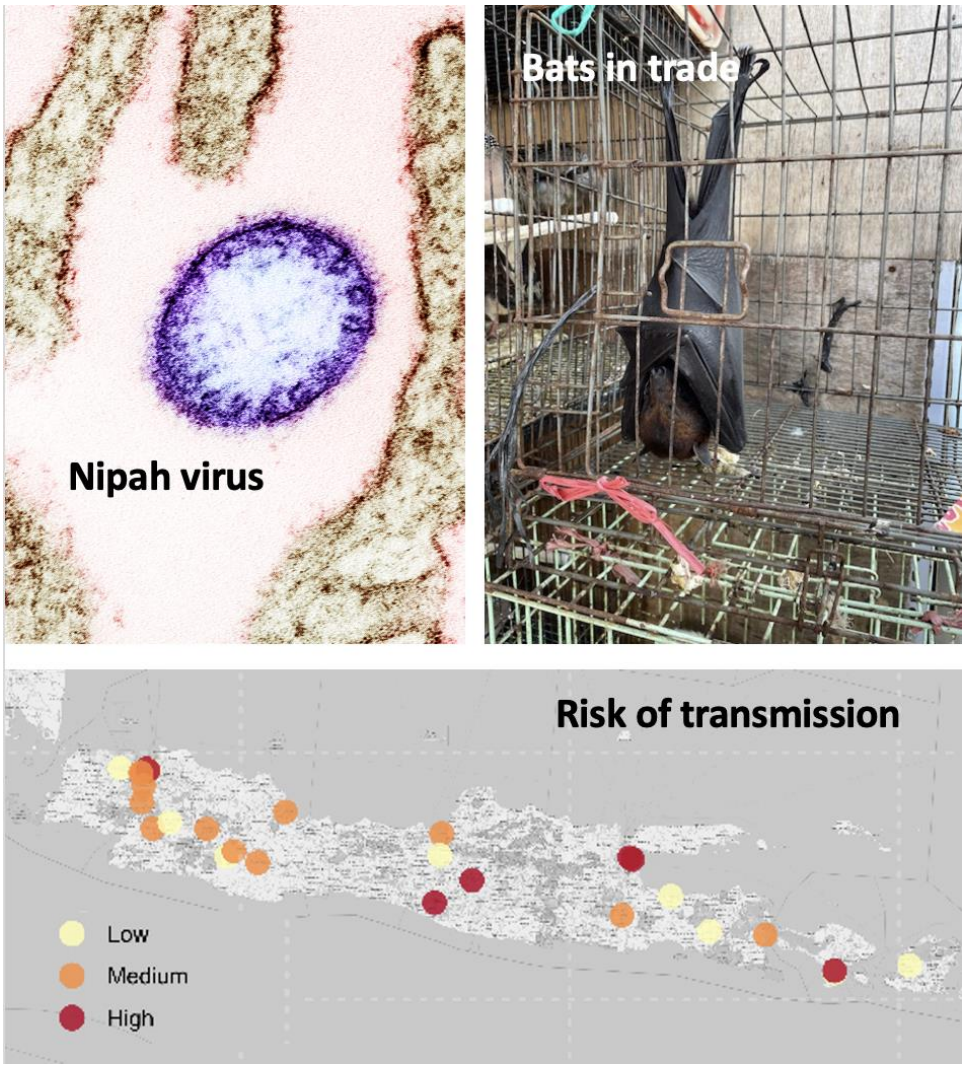
Sydney Merritt: 0000-0002-4039-605X

Nicole A Hoff: 0000-0002-1770-6304

Anne W. Rimoin 0000-0002-0662-9067

Lisa E. Hensley 0000-0003-1188-4342

Graphical Abstract



Highlights [3 to 5 bullet points, each with a maximum of 85 characters, including spaces]

Highlights

Nipah virus is an emerging zoonotic paramyxovirus that can spillover from bats to humans

Wildlife markets in Asia where live bats are sold and slaughtered increase the risk of spillover

We surveyed 29 markets in Indonesia and recorded 2,238 *Pteropus* bats and 1,005 *Cynopterus* for sale

More bats were sold in poorer cities, and in cities with larger Christian populations

Unhygienic condictiones and slaughter on site exacerbate the risk of spillover in markets

Manuscript File
Click here to access/download;Manuscript File;Bats_and_Nipah_23November2025.docx
Click here to view linked References

Bats and Nipah virus: long-term market surveys for live bats in trade in southwestern Indonesia

Vincent Nijman[1], Erly Sintya[2,3,4], Desak Ketut Tristiana Sukmadewi[5], Kuntayuni [2], Sukmasari Triana Gita Putri[5], Jessica Chavez[1,6], Abdullah Abdullah[7], Megan Halbrook[8], Ryan J. Harringan[9], Sydney Merritt[8], Nicole A. Hoff[8], Anne W. Rimoin[8], Lisa Hensley[10]

1 Oxford Wildlife Trade Research Group, School of Law and Social Sciences, Oxford Brookes University, Oxford OX3 0BP, UK
2. Center for Climate Change, Warmadewa University, Denpasar 80239, Bali, Indonesia
3. Faculty of Medicine and Health Sciences, Warmadewa University, Denpasar 80239, Bali, Indonesia
4. School of Chemical, Materials and Biological Engineering, Sheffield University, S1 4LZ, UK
5. Management Department, Faculty of Economics and Business, Warmadewa University, Denpasar 80239, Bali, Indonesia
6. School of Biological and Medical Sciences, Oxford Brookes University, Oxford, UK
7. Department of Biology, Universitas Syiah Kuala, Banda Aceh, Indonesia
8. Department of Epidemiology, University of California, Los Angeles (UCLA), Los Angeles, USA
9. Center for Tropical Research, Institute of the Environment and Sustainability, University of California, Los Angeles (UCLA), Los Angeles, USA
10. Zoonotic and Emerging Diseases Research Unit, United States Department of Agriculture Agricultural Research Service, United States Department of Agriculture, Manhattan, USA

Abstract Bats are important hosts for many zoonotic viruses, including Nipah virus, a bat-borne emerging zoonotic disease. In southwestern Indonesia, bats are sold at marketplaces for traditional Asian medicines, especially as a treatment for asthma. After purchase bats are slaughtered at the market location where they were sold. These markets present a significant risk for Nipah transmission between bats and humans or bats and intermediate species. Between 2012 and 2025 we conducted 348 surveys in 29 animal markets and counted live bats offered for sale. We recorded 2,238 *Pteropus* bats and 1,005 *Cynopterus* bats during 290 (83%) of the surveys, and most markets displayed between 5 and 10 bats, up to 50 bats, at any given time. More bats were displayed on weekends than on weekdays, and over the 14 years covered by our survey trade was stable. There was no observed seasonality in the number of bats for sale. Average asking prices were US$22.25(±1.15) for *Pteropus* bats and US$12.75±4.19 for *Cynopterus* bats. Cities where people had lower purchasing power offered more bats per million people than their more affluent counterparts. Indonesia is the largest Muslim country globally by population, and bats are considered haram (unfit for consumption).

Consequently, we observed a more bats in regions with larger Christian populations. With thousands of people visiting these markets daily, potentially in close contact with bats, we provide evidence that the live bat trade increases the risk of zoonotic disease spillover, not only for Nipah virus but also other emerging zoonotic diseases.

Keywords: Chiroptera, Indonesia, paramyxovirus, wildlife trade, zoonotic diseases

1. Introduction

Bats are important hosts for many zoonotic viruses, including Nipah virus, a bat-borne emerging zoonotic paramyxovirus named after Sungai Nipah (a village in Peninsular Malaysia) where the virus was first isolated (Looi & Chua 2007). Since its discovery in 1998/1999, there has been repeated spillover of Nipah virus from bats to people and to livestock, with a high case fatality rate observed in humans (up to 95%, Arunkumar et al. 2019). The virus is especially prevalent in South and Southeast Asia, with human outbreaks occurring annually and seasonally between November and April in countries like Bangladesh (Gurley et al. 2017), although Epstein et al. (2020) noted that transmission there could occur at any time of the year. There are no therapeutics to mitigate or cure the disease and no preventative vaccines for Nipah virus are available. Nipah virus can be transmitted directly to humans by bats, domestic animals (including pigs, dogs and cats), or other infected humans (Chaiyes et al. 2022: Rahman et al. 2024). It can also be transmitted indirectly via bat-contaminated food (e.g., date palm sap or fruit) via domestic animals or other intermediary hosts, including pigs. The main carriers of Nipah virus are flying fox bats of the genus *Pteropus* (Looi & Chua 2007; Chaiyes et al. 2022: Rahman et al. 2024). However, a sero-epidemiological study in Malaysia also found four fruit bat species as carriers of the pathogen, i.e., *Pteropus hypomelanus*, *Pteropus vampyrus*, *Cynopterus brachyotis* and *Eonycteris spelaea* (Yob et al. 2001). The virus has also been recorded in a smaller roundleaf bat, *Hipposideros larvatus,* in Thailand (Wacharapluesadee et al. 2005). Density of livestock, human population density, and deforestation are key factors that impact Nipah virus transmission from bats or intermediate hosts to humans. (Chaiyes et al. 2022; Rahman et al. 2024).

Indonesia has been identified as a high risk location for Nipah virus outbreaks (Rahman et al. 2024), due to the large numbers of potential host bat species, a large and often dense human population, high human contact rates with bats through capture and trade, and increasingly large-scale land use changes, which bring bats and humans in regular close contact. Indonesia is situated in close geographic proximity to three of the countries where Nipah virus outbreaks have been recorded (Malaysia, Singapore and the Philippines).

Three distinct types of bat trade are present in Indonesia: 1) taxidermied bats, 2) bat meat, and 3) live bats. The origin of taxidermied bats is often unclear, but at least some of this trade is

intended for international destinations. These traders are based in Java, yet bats may be sourced from other islands; the bat species most commonly sourced for taxidermy are small, often colourful, species such as *Rousettus* spp., *Hipposideros* spp., and *Kerivoula* spp. (e.g., Chaber et al. 2021; Hunter et al. 2024; Coleman et al. 2024). The trade in bat meat is mostly reported from eastern Indonesia, i.e., the islands of Sulawesi and, to a lesser degree, Papua. The main species are the larger flying foxes, e.g., *Pteropus* spp and *Acerodon* spp. and small fruit bats (*Cynopterus* spp., *Rousettus* spp., *Nyctimene* spp., *Thoopterus* spp., and *Styloctenium* spp.) present in some of the markets (Sheherazade and Tsang 2015; Pangau-Adam et al. 2012; Kamilin et al. 2022; Lee et al. 2005; Mickelburgh et al. 2009; Latinne et al. 2020; Bailey et al. 2022; Ransaleleh et al. 2020). In Sulawesi, the consumption of bats differs between regions, and this is strongly linked to the predominant religion of the area (Christianity versus Islam). Sheherazade & Tsang (2015) found that interviewees in North Sulawesi would consume flying foxes at least once a month, but the frequency increased tenfold around Christian holidays. Similar findings were reported by Latinne et al. (2020). According to vendor survey responses, flying foxes are sold daily, with a 3-to-6-fold increase on Saturdays and Mondays (Sheherazade & Tsang 2015). In Papua, significantly fewer animals were offered for sale during the wet season (October to February) than during the other months (Pangau-Adam et al. 2012). In the markets in Sulawesi and in Papua, almost all the bats were already dead by the time they reached the market, and many were cooked prior to sale (Latinne et al. 2020; Kamilin et al. 2022). Market vendors interviewed by Latinne et al. (2020) stated they had not received live bats for the past few years.

The live trade is concentrated in western Indonesia and especially on the islands of Sumatra, Java and Indonesian Borneo. The main species are mid-sized to large fruit bats, such as *Pteropus* spp and *Cynoptherus* spp (Morcatty et al. 2022). In Central Kalimantan, the large majority of vendors indicated that there was no specific time of year when they did not sell flying foxes (Harrison et al. 2011). Live bats are traded largely for medicinal purposes, with bats either taken home alive by the buyer or more commonly with the bat being slaughtered by the vendor at the point of sale (Harrison et al. 2011; Morcatty et al. 2022). Within Indonesia, Deka & Morshed (2018) highlighted the islands of Sumatra, Java, Bali and Lombok as areas with a high probability of transmission of Nipah virus to humans.

Of the three types of trade, it is thought that these live trade markets represent the highest relative risk of disease transmission, particular of Nipah viruses to secondary and human hosts, due to the close contact, frequency of interactions with live (potentially virus-harbouring) bat species, and sheer volumes of animals represented in these live markets. While it is assumed that some risk must be present at these live bat markets, it is unclear what the relative risk of these markets may be to local, regional, or international marketgoers, and the extent to which population size, market density,

economic conditions, or cultural practices may affect this risk. To assess the risk of these live trade bat markets to human populations, we performed extensive surveys across multiple markets and seasons to provide new data as to the relative risk that such markets may present to public health, and to better understand measures that could be taken to prevent or mitigate such risk.

Several studies have detected anti-Nipah virus antibodies or viral genomes in bats that were offered for sale in animal markets on these islands (Sumatra: Sendow et al. 2006, 2013; Java Sendow et al. 2006; Putro et al. 2025; Indonesian Borneo: Sendow et al. 2010) showing there is a real risk of transmission in these markets. With this in mind, we set out to explore the dynamics of the live bat trade in western Indonesia based on a sustained monitoring programme that ran for over a decade. We evaluate some of the associations that have been reported in other studies (as summarised above), including spatial and temporal patterns and links to consumer purchasing power and religion (Table 1).

Table 1. Series of null hypotheses concerning the trade in live bats in southwestern Indonesia

Hypothesis	Rationale (reference)	What is tested	Statistics
Survey effort is not related to the proportion of surveys that recorded bats or the mean number of bats that was recorded	Markets were not selected nor surveyed specifically for bats, but a wide range of species were recorded (Morcatty et al. (2022)	Survey effort ~ positive surveys / mean number of bats (large and small pooled)	Pearson's correlation coefficient; surveys (log transformed), proportion (arcsin transformed), mean number (log x+1 transformed)
There is no temporal difference in the number of bats present in markets	There is no bat capturing season; all days of the week are equal (Sheherazade & Tsang 2015)	Mean number of bats (large and small pooled) ~ month / day of the week	Chi^2 test (could be done on the smallest sample size [19 for months; 21 for days of the week]
There is no change in the bat trade over time	No changes have occurred in bat conservation status nor bat protected status	Three markets with coverage over 12+ years [both genera combined]	Pearson's correlation coefficient; Julian date
Numbers of small and large bats do not differ geographically	The study region is somewhat homogeneous in terms of religion and purchasing power (Latinne et al. 2020)	Northwest (Sumatra, Banten, Jakarta), West (West Java), Central (Cirebon, Central Java and Yogyakarta), East (East Java, Bali, Lombok)	ANOVA for independent means
There is no link between the number of bats offered for sale and religion	Christianity does not prohibit the consumption of bats, whereas other religions do (Sheherazade & Tsang 2015; Latinne et al. 2020)	Number and percentage of Christians in a city ~ mean number of bats (pooled) recorded per survey per million people	Pearson's correlation on log-transformed and arcsin-transformed data
There is no link between the number of bats offered for sale and consumer purchasing power	Bats are relatively cheap and are affordable to all	Minimum wage for each city ~ bats per million people	Pearson's correlation on log-transformed data

2. Methods

2.1 Data collection

Between February 2012 and August 2025 we conducted 348 surveys of 29 animal markets to identify the presence of live bats; markets were included if they were surveyed at least twice over this period and if we had detected at least one bat offered for sale (thus excluding markets where the focus clearly was on other wildlife such as reptiles or songbirds). While generally referred to as bird markets (*pasar burung* in Indonesian), or sometimes (domestic) animal markets (*pasar satwa*, *pasar hewan*), a wide range of species are offered for sale at these sites (Croes et al. 2012; Nijman et al. 2009, 2023; Morcatty et al. 2022; Nijman and Lee 2016; Abdullah et al. 2024); we refer to them as animal markets. We conducted surveys in the following provinces: North Sumatra (1 market), Banten (1 market), the Capital District of Jakarta (5 markets), West Java (9 markets), Central Java (3 markets), The Special Region of Yogyakarta (1 market), East Java (6 markets), Bali (2 markets) and West Nusa Tenggara (1 market) (Figure 1).

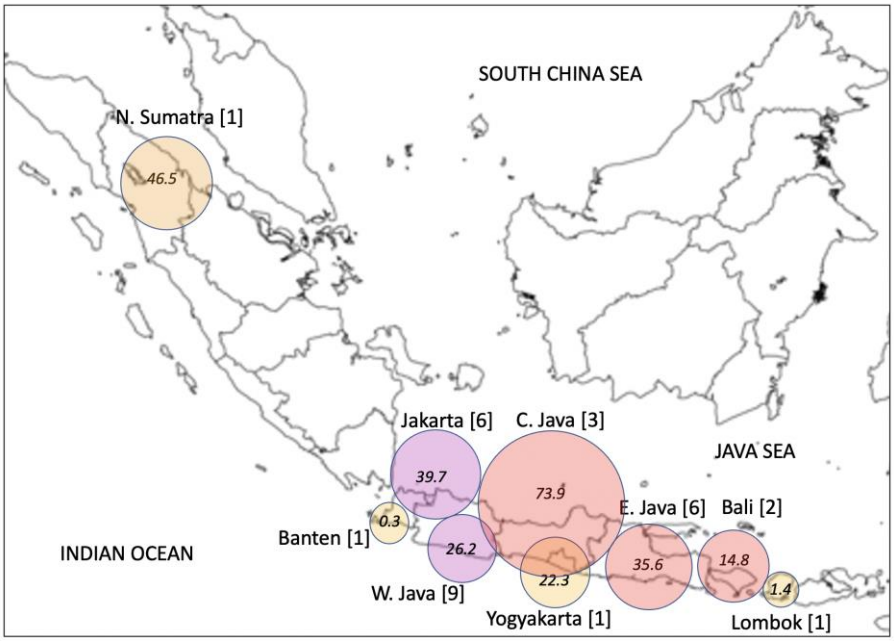


Figure 1. Live bats in Indonesian markets by province, with the number of markets included in each province in square brackets; the size of the circle is proportional to the number of records (and the overall mean is presented in italics within each circle); the color indicates survey effort, with yellow 2-10 surveys; red 20-25 surveys; purple 107 to 151 surveys

Bats are traded openly in the animal markets (Figure 2) and consequently, no covert techniques were needed or used to obtain data on their trade (Morcatty et al. 2022). During market surveillance, surveyors were never offered bats that prior to entering the shop were kept in

backrooms, nor were otherwise out of sight. Surveyors walked slowly through markets, recording numbers and species (non-domesticated mammals, selected birds) on mobile phones or by hand in a notebook (Morcatty et al. 2022; Nijman et al. 2023; Abdullah et al. 2024). Survey teams were comprised of one to three people, with good bat identification skills. Bats are easily identifiable when in the open; in the wildlife markets some of the bats were held higher up and cages may have been tucked away in dark corners (but not hidden or concealed), sometimes hampering identification. Surveys took place on all days of the week – although we were not able to quantify this, we qualitatively noted that the number of visitors to the animal markets was higher on weekends than on weekdays and there is the possibility that the clientele differs during these periods. We did not purchase any bats as part of our survey work, but we did engage with informal discussions about the trade in bats with shopkeepers and owners. Given that many of the markets were visited regularly over several years, study staff built up a rapport with the long-term traders, thus facilitating an honest exchange of information.

Figure 2. Live bat trade in western Indonesia, clockwise from top left: Large flying fox *Pteropus vampyrus* at in Pramuka market, Jakarta; Indonesian short-nosed fruit bat *Cynopterus titthaecheilus* in Pasty, Yogyakarta; lesser short-nosed fruit bat *C. brachyotis* at Jatinegara market, Jakarta; Jatinegara market; large flying fox caged next to a long-tailed macaque *Macaca fascicularis* at Pujasewa, Banyuwangi; Sukahaji market, Bandung (photos: V Nijman).

2.2 Analysis

We included repeat surveys from the same markets that were recorded at least one month apart, as we expect that all bats would have been sold within this period and hence each record would

represent a different individual animal. For each market, we calculated the mean number of bats per survey. We obtained data on the city's human population size (2020), the government recommended monthly minimum wage (2025), and the demographic breakdown of religious affiliations in each city from Badan Statistik Indonesia (BPS 2025). For three markets (Jatinegara in Jakarta, Sukahaji in Bandung, and Satria in Denpasar) that were monitored routinely over 12 years, we tested if the number of bats recorded per survey changed over time.

Prices were collected in Indonesian Rupiahs (IDR) and corrected for inflation to August 2025, so that IDR100,000 in January 2012 equals IDR154,690 in August 2025. This was then converted to US dollars, using an exchange rate of IDR16,788 to the dollar. For statistical tests we refer to Table 1 and we present means ± standard error of the mean (s.e.m).

Based on our observations, a simplified risk value system was developed to provide a first assessment of the possible Nipah virus spillover in bat-associated animal markets. Five main factors were incorporated in the framework: (1) the frequency of bat sightings recorded during the survey; (2) the average number of bats observed at each market; the presence of (3) *Pteropus* and (4) *Cynopterus* bats; and (5) the projected market physical size. Each factor is valued from the lowest risk (1) to the highest risk (3) of potential Nipah virus spillover (Table 2). To quantify the composite risk of Nipah virus spillover for each market, a Weighted Mean Average (WMA) score was calculated (Perry 2011). This involved assigning specific weights to each of the five risk factors, reflecting their perceived importance in contributing to spillover risk:

$$WMA = \frac{P1 \times W1 + P2 \times W2 + \ldots + Pn \times Wn}{W1 + W2 + \ldots + Wn}$$

The collected data, including individual factor scores and the composite WMA scores for each market, were tabulated (Table 2). The analysis involved comparing WMA scores across markets, identifying markets within each risk category, and examining the contribution of individual risk factors to the overall risk profile of the markets. This allowed for the identification of dominant trends and characteristics associated with higher Nipah virus spillover risk.

A weighted moving average method was used to calculate a composite risk score for each market (Table 2). This average provided a standardized measure of relative risk across markets and was subsequently used to classify each site into low, moderate, or high-risk categories. Averages of the five-factor scores produced a definitive risk score for every market. This average provided a consistent evaluation of relative risk across markets and was then used to classify every site into low, moderate, or high-risk categories. Markets were classified into three risk levels based on their Nipah risk spillover score: (high risk) score between 19.25 and 24.33, (medium risk) score between 12.68 and 19.24, and (low risk) Nipah risk spillover score less than 12.68 (Supplementary Appendix I).

198

199 **Table 2.** Market-level factors influencing the potential for Nipah virus spillover in animal markets
200 where bats were offered for sale.

Bats presence	Score	Mean number of bats	Score
Always (95-100%) present	3	more than 10	3
between 51 and 94%	2	between 5 - 10	2
below 50%	1	less than 5	1
Genera present	**Score**	**Size of market**	**Score**
Both genera present	3	More than 0.5 hectare	3
Only *Pteropus* bats	2	Between 0.1 to 0.5 hectare	2
Only *Cynoptherus* bats	1	Less than 0.1 hectare	1

201

202

203 **3 Results**

204 **3.1** ***Presence of bats in markets***

205 We recorded a total of 2,238 *Pteropus* bats and 1,005 *Cynopterus* bats during 290 of the 348 surveys of
206 29 animal markets in southwestern Indonesia (Table 2). The majority of the *Pteropus* bats were
207 identified as large flying foxes (*P. vampyrus*), and the *Cynopterus* bats that we were able to identify
208 were a combination of greater short-nosed fruit bat *C. sphinx*, lesser short-nosed fruit bat *C. brachyotis*,
209 and Indonesian short-nosed fruit bat *C. titthaecheilus*.

210 Large flying foxes were almost twice as expensive as the smaller fruit bats, i.e., averaging
211 US$22.25±1.15 vs US$12.75±4.19, respectively; we note, however, that these are all initial quotes and
212 negotiating to lower prices is a very common practice in these markets making it likely that the final
213 purchasing prices are considerably lower. This is especially true when multiple bats are purchased in
214 a single transaction.

215 On average, each market was surveyed 11.9±2.7 times during the 13.5-year period, but there
216 were large differences between markets, with five markets surveyed twice (minimum for study
217 inclusion) and three markets surveyed over 40 times. Four markets were surveyed over the course of
218 one year only (with at least one month between surveys), and the time between the first and the last
219 survey for the remaining 25 markets was between 2 and 13 years (mean 7.2±0.7 years). There was no
220 relationship between survey effort and the mean number of bats we recorded (Pearson's correlation,
221 R=0.2459, N=29, P=0.1985) nor between survey effort and the proportion of surveys that yielded
222 records of bats (Pearson's correlation, R=0.3006, N=29, P=0.113). Hence, there is no evidence that
223 markets were selectively targeted for either presence or abundance of bats.

224 Giving each market the same weight, we recorded a mean number of 5.6±1.9 *Pteropus* bats per
225 survey and a mean number of 3.5±1.3 *Cynopterus* bats per survey; on average we recorded 10.1±2.6
226 bats per survey. There was a weak but significant positive relation between the number of *Pteropus*

and *Cynopterus* bats recorded in the markets (Pearson's R=0.1373, P=0.0175). In 7 of the 29 markets, we only recorded *Pteropus* bats, and in other 7 of 29 markets only *Cynopterus* bats, and in the remaining 15 markets species of both genera were recorded (Table 3).

The trade in live bats was primarily noted for medicinal purposes (not as part of the pet trade), with asthma treatment being most frequently cited as its benefits. These markets largely advertised, and were targeted to, Indonesian buyers. Additionally, information from traders suggests that all bats are sourced from within Indonesia, and we did not receive any information that bats were sourced from neighbouring countries. However, given the large numbers of bats in major cities (including in 4 of the 5 largest cities in Indonesia, viz. Jakarta, Surabaya, Bandung, Medan), that could not be sourced locally (it is unlikely that short-nosed fruit bats and/or large flying foxes reside in these cities), these bats had to have been transported over large distances prior to reaching the markets. In the markets, bats were either displayed as single individuals in a cage, or in larger groups (up to 12 individuals). In most markets it only one or two traders offered bats for sale; these same traders also often offered plantain squirrels *Callosciurus notatus*, treeshrews *Tupaia* spp and tokay geckos *Gecko gekko* for sale, all of which are also primarily sold to be used in traditional Asian medicine. Other commonly offered species offered for sale alongside the bats were long-tailed macaques *Macaca fascicularis* and Sunda leopard cats *Prionailurus javanensis*, but these are mainly sold as pets. Most animal markets also offered domestic dogs and cats for sale, both known hosts for Nipah virus; in about half the markets cats and dogs were caged in the same parts of the markets where the bats were offered for sale.

It was common for bats to be displayed in the full sun, with no or little shade, close to passing potential customers, often with discarded fruit on the cage floor. Bat cages were typically stacked on top of other cages, either containing more bats, or other wild-caught mammals (e.g., macaques, squirrels, small carnivores), domestic mammals (cats, dogs, hamsters) or birds (e.g., owls, songbirds, domestic chickens).

Upon purchase the bat trader would in most cases slaughter the bat, often in front of the customer, skin it, allowing the buyer to bring the carcass home. The resulting Nipah risk spillover score for the surveyed markets ranged from a minimum of 6.11 (observed at Pasar Hayam, Cianjur, and Mangunhardjo, Probolinggo) to a maximum of 24.33 (observed at Depok, Surakarta, and Pasty, Yogyakarta) (Table 3). The assessment reveals an alternative risk landscape in southwestern Indonesia. Major cities such as Jakarta, Surabaya, Yogyakarta, Surakarta, and Denpasar contain high-risk marketplaces. Medium-risk markets are geographically distributed and are located in cities such as Medan, Bandung, and Malang. Low-risk markets exhibit certain underlying risk characteristics despite having the lowest Nipah risk spillover score in our analysis. This distribution indicates that

various market conditions across the studied regions all possess factors of varying risk contributing to the potential for Nipah spillovers.

Table 3. Overview of live bats recorded in 29 animal markets on the islands of Sumatra, Java, Bali and Lombok over the period 2012-2025.

Province / City / Market	Surveys (years) % bats present	*Pteropus* bats, mean±sem (total)	*Cynopterus* bats, mean±sem (total)	Combined bats when present, mean±sem (total)	Risk Score
NORTH SUMATRA					
Bintang, Medan	2 (2012, 2023) 100	46.50±1.50 (93)	0	46.50±1.50 (93)	16.22
BANTEN					
Curug, Tanggerang	3 (2019) 33	0.33±0.33 (1)	0	1.00±0.00 (1)	8.22
DKI JAKARTA					
Pramuka, Jakarta	35 (2012-2020) 86	17.25±3.01 (604)	2.23±1.03 (82)	23.62±3.13 (686)	22.22
Barito, Jakarta	25 (2012-2019) 100	1.60±0.33 (40)	2.20±0.49 (55)	3.80±3.70 (95)	16.22
Cipinang, Jakarta	3 (2018-2019) 33	0	0.67±0.67 (2)	2.00±0.00 (2)	6.22
Jatinegara, Jakarta	41 (2012-2024) 98	11.37±1.63 (466)	3.56±0.94 (147)	15.33±1.51 (613)	24.22
Kebayoran Lama, Jakarta	3 (2014-2019) 33	0.67±0.67 (2)	0	2.00±0.00 (2)	12.22
WEST JAVA					
Plenongan, Depok	3 (2019) 100	2.00±0.58 (6)	0	2.00±0.58 (6)	16.22
Empang, Bogor	7 (2015-2020) 100	3.86±1.22 (27)	0.71±0.71 (5)	4.57±1.86 (32)	16.22
Pasundan, Sukabumi	4 (2019-2025) 25	0.50±0.50 (2)	0	2.00±0.00 (2)	12.22
Pasarhayam, Cianyur	2 (2019) 50	0	1.5±1.5 (3)	3.00±0.00 (3)	6.11
Sukahaji, Bandung	55 (2012-2024) 87	5.84±1.06 (321)	1.44±0.42 (79)	8.33±1.07 (400)	18.22
Bayongbong, Garut	2 (2018-2022) 100	0	2.50±1.50 (5)	2.50±1.50 (5)	10.22
Kerkhof, Garut	45 (2014-2022) 80	1.82±0.21 (82)	0	2.28±0.21 (82)	16.11
Cikurubuk, Tasikmalaya	17 (2013-2019) 88	0.29±0.17 (15)	2.23±0.42 (38)	2.87±0.40 (53)	14.33
Plered, Cirebon	16 (2016-2020) 88	3.44±0.68 (55)	0.10±0.13 (15)	3.89±0.57 (70)	14.22
CENTRAL JAVA					
Karimata, Semarang	10 (2017-2019) 60	1.91±0.60 (10)	14.6±6.05 (146)	26.17±7.64 (156)	18.22
Pon, Semarang	4 (2017-2019) 50	0.50±0.50 (2)	1.00±1.00 (4)	3.00±1.00 (6)	12.11
Depok, Surakarta	6 (2017-2019) 100	25.00±6.18 (150)	31.67±19.69 (190)	56.67±20.14 (340)	24.33
DI YOGYAKARTA					
Pasty, Yogyakarta	10 (2014-2024) 100	11.20±5.19 (112)	11.50±4.41 (190)	22.70±5.24 (227)	24.33
EAST JAVA					
Bratang, Surabaya	4 (2015-2018) 100	11.50±1.50 (46)	0	11.50±1.50 (46)	24.22
Kupang, Surabaya	4 (2015-2018) 100	0.50±0.50 (2)	15.50±12.50 (62)	16.00±12.00 (64)	20.22
Mangunhardjo, Probolinggo	3 (2013-2018) 33	0	0.67±0.67 (2)	2.00±0.00 (2)	6.22
Splindit, Malang	4 (2015-2020) 75	2.25±1.31 (9)	0	3.00±1.53 (9)	14.22
Sawahan, Jember	2 (2018) 50	0	0.50±0.50 (1)	1.00±0.00 (1)	6.22
Pujasewa, Banyuwangi	3 (2013-2018) 67	1.00±1.00 (3)	3.67±1.86 (11)	7.00±2.00 (14)	16.22
BALI					
Sanglah, Denpasar	12 (2013-2025) 33	0	0.45±0.21 (5)	1.25±0.25 (5)	6.33
Satria, Denpasar	16 (2013-2025) 88	12.47±2.22 (189)	1.87±0.88 (28)	16.54±0.25 (215)	22.22
LOMBOK					
Sindu, Mataram	8 (2018-2025) 71	0.13±0.13 (1)	1.43±0.53 (10)	2.00±0.55 (10)	8.22

3.2 *Bat trade in relation to city's characteristics*

We found no difference in the mean number of bats recorded by geographic location (northwest, west, central and eastern) in southwestern Indonesia (Anova, P=0.285). The cities included in our survey differed by two orders of magnitude in their human population ranging from just over 100,000 (Banyuwangi) to over 10 million (Jakarta). There was a positive relationship between the mean number of bats we recorded in a city and human population size (Pearson's correlation, R=0.4845, N=21, P=0.026). Hence, all subsequent analysis is based on the number of bats per million people in each city.

The government recommended monthly minimum wage for 2025 for the 21 cities we surveyed ranged from US$135 (Yogyakarta) to US$321 (Jakarta), with a mean of US$211±14. There was negative relationship between a city's recommended minimum wage and the mean number of bats per million people as recorded in the markets (Pearson's correlation, R=-0.4738, N=21, P=0.030).

In Indonesia, 87% of the population practice Islam, and about 10% of the population is Christian (BPS 2025), but there are large regional differences. Our sample of 21 cities had relatively high proportions of Christians (e.g., Medan 24.8%, Surakarta, 20.3% Yogyakarta, 15.9% and Jakarta 12.5%) and others a low proportion (e.g., Tasikmalaya 1.1%, Garut 1.1%, Mataram 2.3%). We found a clear positive relationship between the percentage of Christians and the mean number of bats per million people we recorded in the markets (mean 7.9±1.4%) (Pearson's correlation, R=0.4707, N=21, P<0.0313) but not between and the absolute number of Christians living in a city (mean 160,000±7,000) and the mean number of bats per million people in the markets (Pearson's correlation, R=-0.2344, N=21, P<0.3064).

3.3 *Seasonality and change over time*

Each day of the week was not sampled at an equal frequency (χ^2=65.329, df=1, P<0.0001); this was largely driven by fewer surveys having been conducted on a Friday (19 compared to an expected 49 surveys if each day of the week was covered equally). However, the mean number of bats we recorded on Friday to Sunday (mean 9.8±0.8 bat / survey) was higher than during the remaining weekdays (6.5±0.3) (Figure 3).

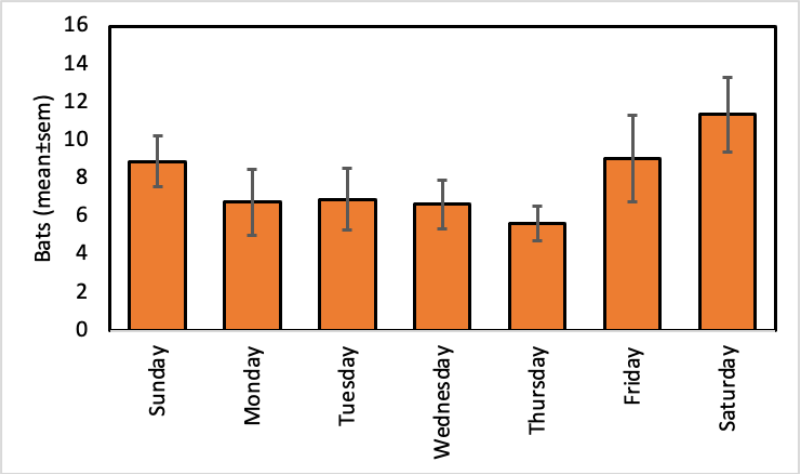


Figure 3. Mean (±sem) number of bats observed in markets by day of the week

As with the days of the week, over the 13.5 year study period, surveying of certain months was more frequent than others, and this was especially apparent for the month of January, which was surveyed twice as much as other months. There was, however, no relationship between the number of surveys and the mean number of bats recorded during each month (Pearson's R=0.3014, N=12, P=0.2412). Overall, there was no clear pattern or seasonality in the mean number of bats recorded each month over the course of the year.

Combining data from all surveys there does not appear to be a change over time in the number of either *Pteropus* or *Cynopterus* bats offered for sale in the markets in southwestern Indonesia (*Pteropus*, Pearson's R=-0.0869, P=0.134 and *Cynopterus*, Pearson's R=0.0577, P=0.320). However, if we focus on three markets that were surveyed most frequently over the entire study period, we see that in Bandung the number of bats recorded has remained stable (Pearson's R=-0.0876, N=54, P=0.5288), in Jatinegara it has declined (although not significantly, Pearson's R=-0.3053, N=40, P=0.0554), and in Satria the number of bats also declined (significantly, Pearson's R=-0.6505, N=15, P=0.0086).

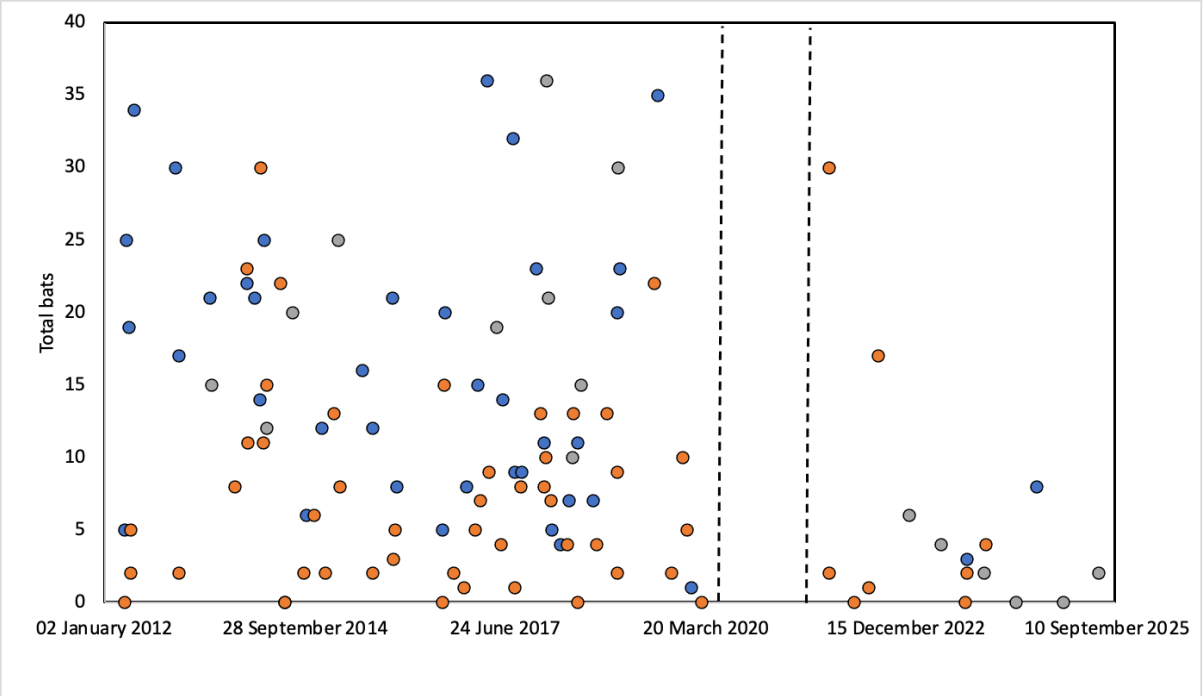


Figure 4. Number of bats recorded in three wildlife markets, i.e., Jatinegara in Jakarta (blue), Sukahaji in Bandung, West Java (orange) and Satria in Denpasar, Bali (grey). The dotted lines indicate the period where no surveys were conducted because of travel restrictions due to Covid-19.

4. Discussion

4.1 Presence of bats in markets and the risk of Nipah spillover

We recorded over 2,000 *Pteropus* fruit bats and over 1,000 *Cynophterus* bats in 83% of our surveys, demonstrating a nearly ubiquitous presence of live bats in the markets of southwestern Indonesia. While there were differences between markets, on average ~10 bats were recorded per survey when bats were present in the market, and both *Pteropus* and *Cynoptherus* species were present in large numbers. Across our study, the larger the city where the market was found, the more bats were offered for sale at any given time.

These bats are typically sold for medicinal purposes by specialized traders in the market, making their presence in the markets highly localized. Once corrected for a city's population size, we found a clear relationship between purchasing power and the number of bats that were offered for sale. In poorer regions there were more bats for sale per million people than the more affluent areas; this may reflect a reliance on traditional medicine, including traditional medicine containing bats (Mardiastuti et al. 2021; Tackett et al. 2022).

Religion was another correlate to the number of bats that were offered for sale in the markets in this part of Indonesia, in that cities with a larger proportion of Christians on average offered more bats per million people for sale. In all the cities we surveyed, Christianity is a minority religion (the

highest percentages were for the cities of Medan and Surakarta but even here it, only 20-25% of the population identified as Christian); Islam is the majority religion in Indonesia except in Bali, where Hinduism is dominant. Consumption of bats for food is forbidden under Islamic tenets, although in Indonesia there is a widespread belief that it is permissible to consume them if it is for medicinal purposes (Kusumaningrum et al. 2022; Mardiastuti et al. 2021). While the relationship between bat consumption and Christianity has been widely reported in Sulawesi, where bats are primarily traded for food and where Christianity is the most prominent religion in certain provinces (Lee et al. 2005; Sheherazade & Tsang 2015; Latinne et al. 2020), it is informative to see the same pattern emerge in southwestern Indonesia, where Islam is the predominant.

The presence of substantial numbers of live bats during most of the surveys we conducted points to widespread exposure of local populations, including collectors, slaughterers, vendors and consumers, to these animals, and increased the risk of zoonotic infection through human-animal interactions. Knowledge of the risks of zoonotic disease transmission in these markets is limited, as is behaviour to reduce these risks (Kusumaningrum et al. 2022; Shepherd et al. 2020; Abdullah et al. 2024).

4.2 *Risk of Nipah virus spillover*

Markets can serve as dynamic ecosystems where several factors contribute towards zoonotic spillover risk: viral transmission between animals and buyers/sellers, the convergence of infected animals causing infection of intermediary hosts, and contaminated objects and fomite transmission (Galindo-González 2022; Brierley et al. 2022; Ellwanger et al. 2021). The initial outbreak of Nipah virus in Malaysia involved spillover from bats to pigs on farms where fruit trees attracted bats, subsequently leading to transmission to humans (Hauser et al. 2021; Chua 2003). Infected pigs were then traded, resulting in cases among abattoir workers in Singapore (Paton et al. 1999). This illustrates the significant role of agricultural interfaces and trade networks, which often culminate in markets, in the dissemination of Nipah virus.

The evaluation of Nipah virus spread in Indonesian markets exposes a complicated interaction among several natural and human elements. The spatial distribution of high-risk marketplaces in big cities shows that these problems are not isolated, but rather can also develop in urban settings. These risks result from the interconnection of bat population dynamics, environmental market conditions, and possible human exposure routes rather than from one single variable (Elwanger et al. 2021; Ghatak et al. 2023). A bigger market size is naturally linked with more activity and likely more interactions between primary, secondary, and human hosts, which in concert will

also elevate the danger of increased contact with contaminated surfaces. Sellers and buyers of wild bats are at high risk of contact with the virus.

It is crucial to recognize the possible impact of unmeasured confounding variables. The present risk evaluation relies on five distinct observational criteria. Nevertheless, additional factors, including hygiene and sanitation protocols in the markets, the provenance of produce (whether obtained from regions with elevated bat activity or recognized Nipah virus circulation), disposal practices of discarded animal parts (Sheta et al. 2019), and other human behaviours in the market, could substantially influence the actual spillover risk (Chaiyes et al 2022; Galindo-González 2022). The Nipah virus spillover scores offer an important albeit approximate assessment of risk, which could be enhanced by integrating data from these other criteria.

4.2 Seasonality and changes over time

In other parts of Indonesia there are clear seasonal differences in the number of bats that are offered for sale and that are indeed sold (Pangau-Adam et al. 2012), and in Bangladesh, Nipah outbreaks have a clear seasonal component (higher in November to April) (Gurley et al. 2017). While over the years we did observe monthly differences in the mean number of bats that were offered for sale (e.g., in March and November we observed almost twice as many bats on average than in April and October) there was no discernable pattern. Similar to research conducted in North Sulawesi (Sheherazade & Tsang 2015) we did find a clear difference in the number of bats we observed over the weekend (Friday to Sunday) compared to other days of the week, i.e., 9.8 bats / survey vs 6.5 bats / survey. We attribute this to a larger number of visitors to these markets on weekends, increasing the number of potential buyers. For two of the markets in Java that we monitored the longest, we did not see a change in the number of bats offered for sale; one market on Bali that was monitored over this same period did show a decrease, and this is easily attributed to the closure of one shop after 2020, that in the preceding decade consistently offered a substantial number of bats for sale. This also shows that the bat trade in this part of Indonesia is driven by only a small number of traders in each market, typically one to four at most, whose livelihoods may greatly impact the dynamics of disease risk. While asking prices for individual bats were high compared to those in Sulawesi (but almost identical to those reported by Croes et al. (2012) for Jakarta) the overall economic value of the live bat trade in southwestern Indonesia must be relatively small.

What is particularly intriguing is that, despite the widespread presence of live animal markets in Indonesia where bats are openly traded, no major outbreaks of Nipah virus have been reported to date. This raises the question of why such outbreaks have not occurred. One such factor may be differences in transmission pathways: in Indonesia, although bats are traded and consumed,

there is limited presence of intermediate hosts such as pigs (except in certain areas like Bali), and there is no widespread practice of consuming raw date palm sap—both of which are key transmission routes in documented Nipah outbreaks elsewhere. Another may be the characteristics of the virus and local bat species: the virus may be circulating at low levels among bat populations without causing large outbreaks—a phenomenon referred to as silent circulation. Handling and consumption practices may also impact transmission potential: cultural and culinary practices in Indonesia may involve cooking bat meat thoroughly, thereby reducing the risk of viral transmission. It is also possible that sporadic Nipah virus infections are occurring and are going undetected or unreported due to lack of specific surveillance or diagnostic capacity. Nipah virus infection can present symptoms similar to other common diseases in the region, such as dengue fever, encephalitis, or acute respiratory infections. As a result, cases may have been misdiagnosed or underreported. Finally, there may be simply an absence of a suitable spillover event: although risk factors exist, a spillover event (where the virus crosses from bats to humans or livestock) may simply not have occurred under the right conditions.

Although no major outbreaks of Nipah virus have been documented in Sumatra, Java, Bali, or Lombok, the presence of *Pteropus* bats—recognized reservoirs of Nipah virus—and their continued trade in live-animal markets highlight a latent zoonotic risk. The nature of these markets, where human-animal contact is frequent and biosafety practices are often absent, presents opportunities for viral spillover, particularly during periods of high market activity such as weekends. While the overall volume of trade appears modest, the fact that it is sustained by a limited number of traders presents a potential leverage point for surveillance and risk mitigation. Incorporating the monitoring of live bat trade into a broader One Health framework—encompassing trader engagement, disease surveillance, and cross-sectoral collaboration—may be essential to reduce the likelihood of future zoonotic emergence and to enhance early detection capacities at wildlife–human interfaces.

Acknowledgements

We thank members of the Little Fireface Project and the Oxford Wildlife Trade Research Group for help with data collection, and members of the Oxford Wildlife Trade Research Group for valuable feedback and comments, and our colleagues at Oxford Brookes University and Universitas Warmadewa for logistic and administrative support.

Author contributions

Conceptualization: VN, ES, DKTS, K; Data curation VN; Formal analysis VN, ES; Funding acquisition VN, JC, AWR, LH; Investigation VN, ES, DKTS, K, STGP, JC, AA, AWR, LH: Methodology VN, ES,

MH, RJH, SM, NAH, AWR, LH; Project administration VN, K, DKTS, AWR, LH; Resources VN, K, AWR, LH; Supervision VN, K, DKTS, AWR, LH; Visualization VN, ES, JC, AA; Writing – original draft VN, ES; Writing – review and editing VN, ES, DKTS, K, STGP, JC, AA, MH, RJH, NAH, AWR, LH

Funding

This work was supported by Cleveland Zoo and Metroparks Zoo Society, Royal Geographical Society Geographical Fieldwork Grant, Re:Wild, and the United States Department for Agriculture (USDA) Agriculture Research Service (ARS) (USDA ARS NACA number 20230048, grant number 58-3022-2-020). These findings do not represent official views or endorsements of the United States Government.

Ethics

No identifiable information on individuals or businesses were collected during this study. This study did not involve any experiment on animals or research involving human participants, and while we did not require institutional permission for observational research in wildlife markets, they were added to Oxford Brookes University's Register of Activities Involving Animals. Our research in Indonesia was underpinned by Memorandums of Understanding between Oxford Brookes University and Universitas Gajah Mada (Yogyakarta) and Oxford Brookes University and Universitas Warmadewa (Denpasar). For permission over the years, we thank the Indonesian Institute of Sciences (LIPI), the Ministry of Research and Technology (RISTEK) and the National Research and Innovation Agency (BRIN).

References

Abdullah, A., Ardiansyah, A., Balestri, M., Campera, M., Chavez, J., Dewi, T., Fourage, A., Hankinson, E.L., Hedger, K., Leupen, B., Manson, S. 2024. Parrot trade and the potential risk of psittacosis as a zoonotic disease in Indonesian bird markets. *Birds* 5: 137-154.

Arunkumar, G., Chandni, R., Mourya, D.T., Singh, S.K., Sadanandan, R., Sudan, P., Bhargava, B. 2019. Outbreak investigation of Nipah virus disease in Kerala, India, 2018. *Journal of Infectious Diseases* 219: 1867-1878.

Bailey, C., Hilser, H., Siwi, Y., Lawe, Z., Waterman, J., Loffeld, T.A.C., Sampson, H., Tasirin, J., Melfi, V., Bowkett, A.E. 2022. Trends in the bushmeat market trade in North Sulawesi and conservation implications. *Animal Conservation* 25: 4-14.

BPS 2025. Badan Pusat Statistik -Data Sensus. bps.go.id/id.

Brierley, L., Vonhof, M.J., Olival, K.J., Daszak, P., Jones, K.E. 2022. Quantifying global drivers of zoonotic bat viruses: A process-based perspective. *American Naturalist* 187:1–19.

Chaber, A.L., Amstrong, K.N., Wiantoro, S., Xerri, V., Caraguel, C., Boardman, W.S., Nielsen, T.D., 2021. Bat E-commerce: insights into the extent and potential implications of this dark trade. *Frontiers in Veterinary Science* 8, 651304.

Chaiyes, A., Duengkae, P., Suksavate, W., Pongpattananurak, N., Wacharapluesadee, S., Olival, K.J., Srikulnath, K., Pattanakiat, S., Hemachudha, T., 2022. Mapping risk of Nipah virus transmission from bats to humans in Thailand. *EcoHealth* 19: 175-189.

Chua KB. 2003. Nipah virus outbreak in Malaysia. Journal of Clinical Virology 26: 265–275.

Coleman, J.L., Randhawa, N., Huang, J.C.C., Kingston, T., Lee, B.P.Y., O'Keefe, J.M., Rutrough, A.L., Thong, V.D., Tsang, S.M., Shepherd, C.R. 2024. Dying for décor: quantifying the online, ornamental trade in a distinctive bat species, *Kerivoula picta*. *European Journal of Wildlife Research 70*: 75.

Croes, J.J., Milner-Gulland, E.J., Shepherd, C.R., 2012. Closing shop. An analysis of cultural, spatial and temporal trends of Indonesian wildlife markets through traders' eyes. University College London, London, UK.

Deka, M.A., Morshed, N., 2018. Mapping disease transmission risk of Nipah virus in South and Southeast Asia. *Tropical Medicine and Infectious Disease* 3: 57.

Epstein, J.H., Anthony, S.J., Islam, A., Kilpatrick, A.M., Ali Khan, S., Balkey, M.D., Ross, N., Smith, I., Zambrana-Torrelio, C., Tao, Y., Islam, A., 2020. Nipah virus dynamics in bats and implications for spillover to humans. *Proceedings of the National Academy of Sciences* 117: 29190-29201.

Ellwanger, J.H., Artur, J., Chies, B. 2021. Zoonotic spillover : Understanding basic aspects for better prevention. *Genetics and Molecular Biology* 1: 1–18.

Galindo-González, J. 2022. Live animal markets: Identifying the origins of emerging infectious diseases. *Current Opinion in Environmental Science and Health* 25: 100310.

Ghatak S, Srinivas K, Arun A, Milton P, Priya GB, Das S, et al. 2023. Limiting the spillover of zoonotic pathogens from traditional food markets in developing countries and a new market design for risk-proofing. *Epidemiology and Health* 45: 2023097.

Gurley, E.S., Hegde, S.T., Hossain, K., Sazzad, H.M., Hossain, M.J., Rahman, M., Sharker, M.Y., Salje, H., Islam, M.S., Epstein, J.H., Khan, S.U., 2017. Convergence of humans, bats, trees, and culture in Nipah virus transmission, Bangladesh. *Emerging Infectious Diseases*, 23: 1446.

Harrison, M.E., Cheyne, S.M., Darma, F., Ribowo, D.A., Limin, S.H., Struebig, M.J., 2011. Hunting of flying foxes and perception of disease risk in Indonesian Borneo. *Biological Conservation* 144: 2441-2449.

504 Hauser, N., Gushiken, A.C., Narayanan, S., Kottilil, S., Chua, J.V., 2021. Evolution of Nipah virus
505 infection: past, present, and future considerations. *Tropical Medicine and Infectious Disease* 6: 24.
506 Hunter, S.B., Weeds, J., Mathews, F., 2024. Monitoring the trade in bat taxidermy and specimens on e-
507 commerce platforms. *Biological Conservation* 299: 110827.
508 Kamilin, A.F., Warsono, I.U., Pattiselanno, F. 2022. Percentage of carcass and habitat of the black bat
509 (*Pteropus alecto*) in Kaironi, Sidey District, Manokwari, West Papua, Indonesia. *Prosiding Seminar*
510 *Nasional Masyarakat Biodiversitas Indonesia* 8: 159-163
511 Kusumaningrum, T., Latinne, A., Martinez, S., Kalengkongan, J., Wiyatno, A., Dewantari, A.K.,
512 Kasenda, N., Bernadus, J.B., Jaya, U.A., Ma'roef, C.N., Francisco, L. 2022. Knowledge, attitudes,
513 and practices associated with zoonotic disease transmission risk in North Sulawesi, Indonesia. *One*
514 *Health Outlook* 4: 11.
515 Latinne, A., Saputro, S., Kalengkongan, J., Kowel, C.L., Gaghiwu, L., Ransaleleh, T.A., Nangoy, M.J.,
516 Wahyuni, I., Kusumaningrum, T., Safari, D., Feferholtz, Y., 2020. Characterizing and quantifying
517 the wildlife trade network in Sulawesi, Indonesia. *Global Ecology and Conservation* 21: 00887.
518 Lee, R.J., Gorog, A.J., Dwiyahreni, A., Siwu, S., Riley, J., Alexander, H., Paoli, G.D., Ramono, W. 2005.
519 Wildlife trade and implications for law enforcement in Indonesia: a case study from North
520 Sulawesi. *Biological Conservation* 123: 477-488.
521 Looi, L.M., Chua, K.B. 2007. Lessons from the Nipah virus outbreak in Malaysia. *Malaysian Journal of*
522 *Pathology* 29: 63–67.
523 Mardiastuti, A., Masy'ud, B., Ginoga, L.N., Sastranegara, H., Sutopo, S. 2021. Wildlife species used as
524 traditional medicine by local people in Indonesia. *Biodiversitas* 22: 329-337.
525 Mickleburgh, S., Waylen, K., Racey, P., 2009. Bats as bushmeat: a global review. *Oryx*, 43: 217-234.
526 Morcatty, T.Q., Pereyra, P.E., Ardiansyah, A., Imron, M.A., Hedger, K., Campera, M., Nekaris, K.A.I.,
527 Nijman, V., 2022. Risk of viral infectious diseases from live bats, primates, rodents and carnivores
528 for sale in Indonesian wildlife markets. *Viruses* 14: 2756.
529 Nijman, V., Lee, P.B. 2016. Trade in nautilus and other large marine molluscs as ornaments and
530 decorations in Bali, Indonesia. *Raffles Bulletin of Zoology* 64: 368-373.
531 Nijman, V., Shepherd, C.R., Van Balen, S. 2009. Declaration of the Javan hawk eagle *Spizaetus bartelsi*
532 as Indonesia's National Rare Animal impedes conservation of the species. *Oryx* 43: 122-128.
533 Nijman, V., Nekaris, K.A.I., Shepherd, C.R., Vigne, L., Ardiansyah, A., Imron, M.A., Ni, Q., Hedger,
534 K., Campera, M. Morcatty, T.Q. 2023. Potential mammalian vector-borne diseases in live and wet
535 markets in Indonesia and Myanmar. *Microbiology Research* 14: 116-131.
536 Pangau-Adam, M., Noske, R., Muehlenberg, M. 2012. Wildmeat or bushmeat? Subsistence hunting
537 and commercial harvesting in Papua (West New Guinea), Indonesia. *Human Ecology* 40: 611-621.

538 Paton, N.I., Leo, Y.S., Zaki, S.R., Auchus, A.P., Lee, K.E., Ling, A.E., Chew, S.K., Ang, B., Rollin, P.E.,
539 Umapathi, T., Sng, I. 1999. Outbreak of Nipah-virus infection among abattoir workers in
540 Singapore. *The Lancet* 354: 1253-1256.
541 Putro, D.B.W., Mulyono, A., Rahardianingtyas, E., Ardanto, A., Joharina, A.S., Hidajat, M.C.,
542 Anggraeni, Y.M., Ristiyanto, R., Sari, T.F., Dharmayanti, N.I., Garjito, T.A. 2025. Nipah virus
543 detection in *Pteropus hypomelanus* bats, Central Java, Indonesia. *Emerging Infectious Diseases* 31: 867.
544 Rahman, M.A., Shanjana, Y., Cronmiller, S., Zong, D., Davis, R., Ernest, J., Nguyen, J., Rawa, A.,
545 Thomas, M.R., Islam, M.R. 2024. Risk evaluation and mitigation strategies for potential outbreaks
546 of Nipah virus infection: Evidenced by the recent incidences in Southeast Asian countries. *Health*
547 *Science Reports* 7: 70239.
548 Ransaleleh, T.A., Nangoy, M.J., Wahyuni, I., Lomboan, A., Koneri, R., Saputro, S., Pamungkas, J.,
549 Latinne, A. 2020. Identification of bats on traditional market in Dumoga district, North Sulawesi.
550 *IOP Conference Series: Earth and Environmental Science* 473, 012067.
551 Sendow, I., Ratnawati, A., Taylor, T., Adjid, R.A., Saepulloh, M., Barr, J., Wong, F., Daniels, P., Field,
552 H. 2013. Nipah virus in the fruit bat *Pteropus vampyrus* in Sumatera, Indonesia. *PLoS One* 8: 69544.
553 Sendow, I., Field, H.E., Curran, J., Morrissy, C., Meehan, G., Buick, T., Daniels, P. 2006. Henipavirus in
554 *Pteropus vampyrus* bats, Indonesia. *Emerging Infectious Diseases* 12: 711.
555 Sendow, I., Field, H.E., Adjid, A., Ratnawati, A., Breed, A.C., Darminto, Morrissy, C., Daniels, P. 2010.
556 Screening for Nipah virus infection in West Kalimantan province, Indonesia. *Zoonoses and Public*
557 *Health* 57: 499-503.
558 Sheherazade, Tsang, S.M. 2015. Quantifying the bat bushmeat trade in North Sulawesi, Indonesia,
559 with suggestions for conservation action. *Global Ecology and Conservation 3*: 324-330.
560 Shepherd, C.R., Leupen, B.T., Siriwat, P., Nijman, V., 2020. International wildlife trade, avian
561 influenza, organised crime and the effectiveness of CITES: The Chinese hwamei as a case study.
562 *Global Ecology and Conservation* 23: 01185.
563 Sheta, B., Njabo, K., Harrigan, R., Shafir, S., Smith, T.B. 2019. Leveraging women's knowledge,
564 practices, and behavior to reduce the spread of avian influenza in Egypt. *Journal of Women's Health*
565 *and Development* 2: 37-47.
566 Tackett, E.S., Kingston, T., Sadeghmoghaddam, N., Rutrough, A.L. 2022. Global medicinal use of bats:
567 a systematic literature and social media review. *Diversity* 14: 179.
568 Wacharapluesadee, S., Lumlertdacha, B., Boongird, K., Wanghongsa, S., Chanhome, L., Rollin, P.,
569 Stockton, P., Rupprecht, C.E., Ksiazek, T.G., Hemachudha, T., 2005. Bat Nipah virus, Thailand.
570 *Emerging Infectious Diseases*, 11: 1949.

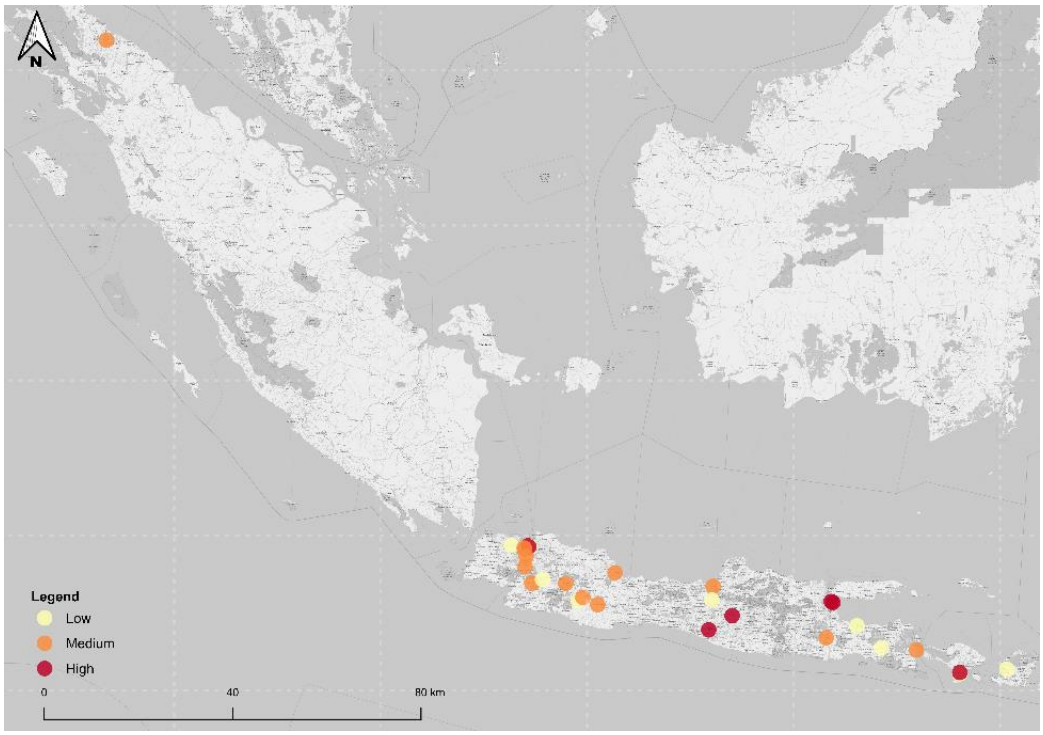
571 Yob, J.M., Field, H., Rashdi, A.M., Morrissy, C., van der Heide, B., Rota, P., bin Adzhar, A., White, J.,
572 Daniels, P., Jamaluddin, A., Ksiazek, T. 2001. Nipah virus infection in bats (order Chiroptera) in
573 peninsular Malaysia. *Emerging Infectious Diseases 7*: 439.
574

575 Appendix I. Composite Risk Score of Nipah Virus Spillover Risk in Animal Markets

Markets	Bat Present	Mean number Pteropus	Mean number Cynoptherus	Presence of Species	Market Size	Nipah spillover score
Bintang, Medan	3	3	0	2	2	16.22
Curug, Tanggerang	1	1	0	2	2	8.22
Pramuka, Jakarta	2	3	3	3	2	22.22
Barito, Jakarta	3	1	1	3	2	16.22
Cipinang, Jakarta	1	0	1	1	2	6.22
Jatinegara, Jakarta	3	3	3	3	2	24.22
Kebayoran Lama, Jakarta	1	1	1	3	2	12.22
Plenongan, Depok	3	1	1	3	2	16.22
Empang, Bogor	3	1	1	3	2	16.22
Pasundan, Sukabumi	1	1	1	3	2	12.22
Pasir Hayam, Cianyur	1	0	1	1	1	6.11
Sukahaji, Bandung	2	2	2	3	2	18.22
Bayongbong, Garut	3	0	1	1	2	10.22
Kerkhof, Garut	3	1	1	3	1	16.11
Cikurubuk, Tasikmalaya	2	1	1	3	3	14.33
Plered, Cirebon	2	1	1	3	2	14.22
Karimata, Semarang	2	1	3	3	2	18.22
Pon, Semarang	1	1	1	3	1	12.11
Depok, Surakarta	3	3	3	3	3	24.33
Pasty, Yogyakarta	3	3	3	3	3	24.33
Bratang, Surabaya	3	3	3	3	2	24.22
Kupang, Surabaya	3	1	3	3	2	20.22
Mangunhardjo, Probolinggo	1	0	1	1	2	6.22
Splendid, Malang	2	1	1	3	2	14.22
Sawahan, Jember	1	0	1	1	2	6.22
Pujasera Karangrejo, Banyuwangi	2	1	2	3	2	16.22
Sanglah, Denpasar	1	0	1	1	3	6.33
Satria, Denpasar	2	3	3	3	2	22.22
Sindu, Mataram	2	0	1	1	2	8.22

576

Appendix II/ Spatial Risk Mapping of Nipah Virus Spillover Potential Across Bats and Human in Animal market, Southwestern Indonesia, 2012-2025.



Declaration of interests

☐The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☒The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Vincent Nijman reports financial support was provided by Cleveland Zoo and Metroparks Zoo Society. Jessica Chavez reports financial support was provided by Royal Geographical Society Geographical. Vincent Nijman and Jessica Chavez reports financial support was provided by ReWild. Lisa Hensley reports financial support was provided by United States Department for Agriculture (USDA) Agriculture Research Service (ARS). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.