**Objective** To better understand the potential risks of Nipah virus emergence in Cambodia by studying different components of the interface between humans and bats.

**Methods** From 2012 to 2016, we conducted a study at two sites in Kandal and Battambang provinces where fruit bats (*Pteropus lylei*) roost. We combined research on: bat ecology (reproductive phenology, population dynamics and diet); human practices and perceptions (ethnographic research and a knowledge, attitude and practice study); and Nipah virus circulation in bat and human populations (virus monitoring in bat urine and anti-Nipah-virus antibody detection in human serum).

**Findings** Our results confirmed circulation of Nipah virus in fruit bats (28 of 3930 urine samples positive by polymerase chain reaction testing). We identified clear potential routes for virus transmission to humans through local practices, including fruit consumed by bats and harvested by humans when Nipah virus is circulating, and palm juice production. Nevertheless, in the serological survey of 418 potentially exposed people, none of them were seropositive to Nipah virus. Differences in agricultural practices among the regions where Nipah virus has emerged may explain the situation in Cambodia and point to actions to limit the risks of virus transmission to humans.

**Conclusion** Human practices are key to understanding transmission risks associated with emerging infectious diseases. Social science disciplines such as anthropology need to be integrated in health programmes targeting emerging infectious diseases. As bats are hosts of major zoonotic pathogens, such integrated studies would likely also help to reduce the risk of emergence of other bat-borne diseases.
Introduction

Infectious diseases remain an important threat to global health, as demonstrated by the recent emergence of coronavirus disease-2019 (COVID-19).\(^1\) The risk of such an emergence was known and in its 2018 list of priority diseases the World Health Organization (WHO) recognized that a serious international epidemic could be caused by a pathogen then unknown.\(^2\) Emerging infectious diseases related to known pathogens also pose a serious threat. For example, Nipah virus has caused recurrent disease outbreaks in Bangladesh and western India\(^3\) and the most recent outbreak in Kerala in 2018 was the first recorded in southern India.\(^4\) Some of these outbreaks involved human-to-human transmission, demonstrating potential for wider spread of this virus causing highly lethal encephalitis.\(^5\) Most emerging infectious diseases are zoonotic and originate in wildlife, and the epidemiology of the disease is often complex.\(^6\) Because multiple factors including environmental and anthropological factors are often involved in the processes of disease emergence,\(^7\) surveillance and control of emerging infectious diseases such as Nipah requires integrated (transdisciplinary and trans-sectoral) approaches in health management.\(^8\)

Fruit bats of the *Pteropus* genus, also known as flying foxes, are the main reservoir for the virus, which makes understanding of their ecology central to any research on Nipah virus emergence.\(^9,10\) Agricultural practices have also been key factors in the emergence of the disease in humans. For instance, in Malaysia, where the first reported Nipah outbreak led to 265 human cases and 105 deaths, intensification of pig farming and cultivation of fruit trees in the same locations was an important determinant of the outbreak. The outbreak was ultimately curtailed by the culling of over 1 million pigs.\(^11,12\) In Bangladesh and India, consumption of raw palm sap is the main route of transmission of the virus to humans.\(^3,13\) Although simple prevention measures such as use of bamboo skirts on trees to prevent bats from accessing the palm sap have been suggested, the adoption of these fences by local communities depends on their perceptions of transmission risks and diseases in general.\(^14\) As a consequence, understanding communities’ perceptions towards bats and diseases is critical to the success of any prevention plan.

Little is known about the circulation of bat-borne diseases in general and of Nipah virus in particular in Cambodia. Though Nipah virus was isolated in 2000 from a *Pteropus lylei* roost in western Cambodia, this finding was never replicated and no human case has been reported in the country.\(^15\) This situation may be similar to Thailand where Nipah virus circulates in *P. lylei* populations but where human and domestic animal cases have never been reported.\(^16\) Over a dozen *P. lylei* roosts are known in Cambodia and most of these are located in villages or cities, which suggests clear interfaces with humans and potential for direct or indirect contact.\(^17\) Studies of Nipah virus circulation in bats – coupled with research on agricultural practices and risk perceptions
within local communities – would shed light on the potential risk for Nipah virus emergence in Cambodia, either through the transmission routes observed elsewhere or due to country-specific factors. Better knowledge would also help to identify human populations at risk who could then be targeted for future surveillance and prevention programmes.

The overall objective of our study was to better understand the potential risks of Nipah virus emergence in Cambodia. We combined research on bat ecology (reproductive phenology, population dynamics and diet); human practices and perceptions (ethnographic research and knowledge, attitude and practice studies); and Nipah virus circulation studies in bat and human populations (virus monitoring in bat urine and anti-Nipah virus antibody detection in human serum). We aimed to: (i) confirm the presence of Nipah virus in bat populations and understand circulation patterns; (ii) determine potential transmission routes for the virus from bats to humans; and (iii) identify potential unreported virus transmission from fruit bats to humans (spillover) and the associated risk factors.

Methods
Our study was undertaken at two sites in rural areas of Kandal and Battambang provinces in Cambodia where large P. lylei populations have been reported (Fig. 1). More details of the location and laboratory methods are in the authors’ data repository.18

Census, diet and reproductive cycle
We conducted monthly censuses from March 2013 to August 2016 to estimate the size of the P. lylei population at the primary study site in Kandal province. An exit census was undertaken on two consecutive evenings every month when the bats emerged from the roost at dusk. During the exit censuses, we used hand-held tally counters to count the bats on the two main routes they used to disperse from the roost each evening.19 The bats were also observed directly with binoculars during the day every month to identify specific phases of their annual reproductive cycle, including mating, parturition and weaning. A study of the diet of P. lylei based on the analysis of faecal samples was also implemented from December 2013 to May 2014 at the primary study site.18

Urine sampling and testing
We undertook research on Nipah virus circulation in P. lylei by testing bat urine samples collected at the primary study site from 2013 to 2016. We performed preliminary sampling each month from March to July 2013 to assess seasonality in the occurrence of Nipah virus, as suggested by a previous study on P. lylei in Thailand.20 We subsequently conducted longitudinal sampling at the same site from March 2014 to September 2016, which comprised 36 sampling sessions separated
by intervals of 3 weeks to 2 months. We also collected urine samples at the secondary study site in Battambang province each month from March to June 2013, and in May 2014 and April and May 2015. The timing of the latter sampling was again chosen to reflect the seasonality of Nipah virus observed in Thailand.\textsuperscript{20} In each sampling session, we collected a target of 100 urine samples with micropipettes over one or two consecutive mornings from plastic sheets laid under the trees where the bats roost. A volume of 0.5 mL of urine was collected per sample which was transferred to cryotubes and immediately stored in liquid nitrogen.

We screened all samples for Nipah virus ribonucleic acid detection using a SYBR® Green reverse transcription polymerase chain reaction (RT–PCR) assay\textsuperscript{21} and suspect samples were tested by a duplex nested RT–PCR method.\textsuperscript{18,22}

**Ethnographic study**

We conducted an ethnographic study at our primary study site in Kandal province to understand local uses and perceptions related to fruit bats, with a specific emphasis on health issues and potential risks for disease transmission from bats to humans. A Khmer-speaking French anthropologist undertook semi-structured interviews with villagers representative of the people potentially exposed to fruit bats. Individual and collective interviews were conducted with the following participants: a group of monks and elders involved in the social and religious life of the Buddhist pagoda where the *P. lylei* roost is located; the head of the pagoda; a fruit-bat hunter; two palm-juice collectors; two mango and sapodilla fruit plantation owners; two fruit sellers at the local market; the owner of a commercial pig farm; and the owner of a pig-breeding farm who also owned a mango plantation. All of the data obtained were transcribed and analysed in a qualitative manner.

**Knowledge, attitude and practice study**

Using the results of our ethnographic study we developed a questionnaire comprehensible to our respondents. The questionnaire was developed in Khmer by our anthropologist and team of epidemiologists and ecologists to obtain quantitative information on the uses and perceptions related to fruit bats in the study area.

We interviewed residents in the primary study area in 2016 at the same time as a *P. lylei* global positioning system (GPS) telemetry study.\textsuperscript{23} Additional residents were selected based on the results of the GPS telemetry in areas where clear interactions between fruit bats and humans were observed, most notably as a result of fruit farming, fruit collection and pig farming.\textsuperscript{23} In addition, a group of residents living within a 10 km radius of the *P. lylei* roost in Battambang province were also interviewed and asked to participate in the serological study.
Serological survey
To identify potentially undetected spillovers of Nipah virus from *P. lylei* to humans in the past, we implemented a serological survey of people with the highest exposure risk to fruit bats at our study sites. The study was first presented to the village authorities and eligible subjects were then selected based on their occupation and the results of the GPS telemetry study.23 Palm juice collectors, fruit farmers and collectors, fruit-bat hunters and people living or working under the roost were specifically targeted. We tested sera for Nipah virus immunoglobulin G antibodies by an in-house enzyme-linked immunosorbent assay.18

Ethics
The study was approved by the Cambodian National Ethics Committee for Human Research (approval #087NECHR/2011). We obtained written informed consent from the participants, or their parent or guardian, for inclusion in the study and for blood sampling.

Results
Population dynamics of *P. lylei*
The monthly estimated population of *P. lylei* at our primary study site ranged from about 2000 to 7000 individuals and increased during the study period (Fig. 2). Mating, parturition and weaning of fruit bats occurred at the same time each year, with mating in November, parturition in April and weaning in June. Pregnancy occurred from December to March, while lactation took place in April and May (Fig. 2). As anticipated, the bat population increased each year after weaning, when annual cohorts of juvenile bats started flying and were consequently recorded in our exit censuses.

Diet of *P. lylei*
We identified seven plant species from the 210 faecal samples collected during the study. These included pollen from flowers of the Malay apple (*Syzygium* spp.), kapok (*Ceiba pentandra*), petai (*Parkia* spp.) and cotton tree (*Bombax ceiba*), seeds from fig trees (*Ficus* spp.) and fibres and pulp of sapodilla (*Manilkara zapota*) and mango (*Mangifera indica*). Pollen belonging to two additional unidentified species were also present in our samples. Pollen from flowers (mainly *Syzygium* spp. and *Ceiba pentandra*) were identified in most samples collected from December 2013 to March 2014, whereas fruit (mainly sapodilla) were most abundant in samples collected in April and May 2014 (Fig. 3).

Nipah virus circulation in *P. lylei*
We collected a total of 3157 urine samples during 36 sampling sessions at the primary study site in Kandal province. Among these, 20 samples (0.6%) were positive for Nipah virus genome detection.
The proportions of positive samples in individual sessions ranged from 0% to 8%, with no clear seasonal pattern of Nipah virus circulation (Fig. 4; data repository). Nonetheless, Nipah virus was detected in female bats during lactation in 2013, 2014 and 2015, and during pregnancy in 2015. Outside of these periods, the virus was only detected in one sampling session in October 2015 and was not detected in 2016, despite 10 sampling sessions undertaken in nine different months. As a result, detection rates of Nipah virus were higher during the reproductive stages of pregnancy and lactation compared with the rest of the year, with 18 out of 1962 (0.9%) and 2 out of 1213 (0.2%) samples positive, respectively (logistic regression, adjusted odds ratio, OR: 5.61; 95% confidence interval, CI: 1.61–35.3).

A total of 773 urine samples were collected during seven sampling sessions at the Battambang roost site. Most of these sampling sessions occurred during the lactation period of female bats with only one session during pregnancy and one following lactation in 2013 (data repository). Overall, eight samples (1.0%) were confirmed positive for Nipah virus and the proportions of positive samples from individual sessions ranged from 0 to 4.5% (data repository).

**Ethnographic study**
Farmers reported that fruit bats ate cultivated fruits but that these nocturnal visits did not bother them because the bats consumed ripe fruit, whereas mango and sapodilla fruit, the most commonly cultivated fruit, are collected before they ripen. As a result, the impact of bats on fruit production was considered negligible by respondents. However, longan (*Dimocarpus longan*), another fruit consumed by bats, was an exception because it is allowed to ripen before harvesting. Farmers consequently reported using nets to protect these fruits from bats.

Fruit bats can drink the juice which flows from palm flowers into collecting containers (typically bamboo vessels or plastic bottles). Due to the small diameter of the upper portion of these containers, however, bats can presumably only access nectar within them when they are full or almost full (data repository).

Study participants reported that fruit bats were not considered a potential source of disease for humans but that it was considered disgusting to eat a fruit partially consumed by an animal. More generally, animals were not considered by participants to be a potential source of diseases for humans, with the exception of a few diseases including rabies, avian influenza and malaria.

According to study participants, the cosmological world is often implicated in human illness. In Cambodia, the dead (*khmoch*) – including ancestors (*daun ta*), evil spirits (*preay*), tutelary spirits linked to particular place (*kru batjeay*) and household gods (*neak ta*) – can all make a person ill. As a consequence, all health care can potentially involve the invisible world in addition
to modern medicines which are also used. For instance, a medical injection may sometimes work by providing an offering to a tutelary spirit who, if offended, might conversely prevent it from working.

Knowledge, attitude and practice study
We interviewed 41 people from 36 households during the GPS telemetry study in Kandal province using the questionnaire. Following the telemetry study, we interviewed and took blood samples from 164 individuals from 41 additional households in Kandal, bringing the total number of households surveyed in the province to 77. In Battambang, we interviewed and sampled 254 people from 103 households. Due to the time required to inform participants about the study, we completed only the three first sections of the questionnaire for participants who also agreed to give blood samples.

The primary difference in main occupation of participants between the two sites was the presence of palm-juice collectors only in Kandal (14; 7.0%) and a greater proportion of bat-guano collectors in Battambang (27 people; 10.6%) than in Kandal (1 person; 0.6%). Numbers of participants raising pigs were similar at both sites and only 16 households reported owning from one to 11 pigs. Table 1 summarizes the key results for practices and perceptions related to potential Nipah virus transmission at the two study sites (data repository).

Serological survey among exposed villagers
Most heads of families were farmers owning fruit trees. Participants who were considered particularly at risk of potential contact with fruit bats and Nipah virus transmission included 14 palm-juice collectors and one palm-juice seller, as well as four fruit-bat hunters. All sera tested (164 in Kandal and 254 in Battambang) were negative for Nipah virus antibodies (data repository).

Discussion
Our integrated research allowed us to consistently collect information on different factors that could be involved in Nipah virus disease emergence among humans in our study areas. First, by combining the results of our study of reproductive phenology and virus monitoring, we confirmed the presence of Nipah virus in bat urine at both study sites. While Nipah virus circulation appears to be intermittent with no clear seasonal pattern, specific periods – notably pregnancy (December to March) and parturition (April–May) – coincided with increased virus detection rates in bats.

Second, by combining the results of our diet study, virus monitoring in bat urine and our ethnographic and knowledge, attitude and practice studies, we identified potential routes for virus transmission from bats to humans through fruit such as mango and sapodilla. These two fruits are
consumed by bats and harvested by humans when Nipah virus is potentially circulating in the bats (April and May). Palm nectar could also act as a transmission route because it is commonly consumed raw by humans and was also reported to be consumed by bats. Furthermore, these practices are mostly conducted in the absence of any perception of zoonotic risks by participants. Finally, the lack of a confirmed Nipah virus spillover based on our serology study of people residing in areas with close bat–human contact enables us to consider the likelihood of Nipah virus emergence in our study areas.

The absence of confirmed antibodies against Nipah virus among study participants could be due to two reasons: an actual absence of previous spillovers or a failure to detect these. These hypotheses are discussed in more detail in the data repository. Nevertheless, our results suggest that Nipah virus spillover would be a rare event in our study sites. Even in Bangladesh, where most Nipah virus outbreaks have occurred to date, Nipah virus infection is rare in humans and suggests that spillover may require temporal alignment of a complex combination of factors that rarely occur. Palm sap, and not palm juice, is collected in Bangladesh using large clay pots. The ease of access to the pots may facilitate contamination by bats. Consumption of palm sap also appears to be more popular in Bangladesh, whereas in our study areas palm juice is preferred but only occasionally consumed. Thus, greater exposure related to these practices in Bangladesh may explain why intermittent shedding of Nipah virus by bats results in recurrent outbreaks in Bangladesh but not in Cambodia.

Our results must be interpreted with caution because we only monitored one fruit-bat colony for 4 years and another one for several months over 2 years. Furthermore, the absence of detection of Nipah virus in 2016 suggests inter-annual variation could also occur, as suggested by serological monitoring in Malaysia. We are still modelling our data set to test different factors that might contribute to this apparent seasonality. Possible factors include a sharp increase in numbers of susceptible juvenile bats or a revival of virus outbreaks in pregnant and lactating female bats. We also aim to explain circulation patterns involving fluctuating herd immunity over several years. The apparent increase in the number of bats in our study colony over the study period is another factor that could be considered in such a model. However, in the absence of population data from nearby roosts, differentiating between the natural growth in numbers and immigration to herds could prove difficult.

Notwithstanding these limitations, our study suggests certain surveillance and control measures would be helpful in Cambodia. For example, Nipah virus should be considered as a potential cause of acute encephalitis in Cambodia and encephalitis patients should be tested for
Nipah virus, particularly in the case of severe infection. In bats, surveillance could also be targeted based on our results which suggest increased Nipah virus circulation occurs when females are pregnant and lactating. As our sampling method did not allow us to collect individual urine samples, we could not estimate the prevalence of the virus in the bat population. However, the increased circulation of Nipah virus during bat pregnancy and lactation suggested by our finding is consistent with observations in Malaysia and Thailand.\textsuperscript{20,25} Thus, pending available resources, Nipah virus surveillance in bats could be intensified in the March to May period. Allied to this, GPS telemetry at our main study site demonstrated that the bats moved relatively frequently to several other roosts located up to 105 km away. This result suggests a global population structure rather than a meta-population structure,\textsuperscript{23} in which case Nipah virus surveillance at a few roost sites might be sufficient to detect virus circulation in the country.

Our results also allow us to propose interventions to limit the exposure of local communities to bats. However, these would involve changes in practices that can be hindered by people’s perception of a low risk of disease. Our ethnographic and subsequent knowledge, attitude and practice study showed that people in our study areas did not perceive risks related to bats and more generally to animals. As in many other Asian countries, health beliefs in Cambodia combine modern medicine and mixing of several religious beliefs and practices, including animistic representations of diseases.\textsuperscript{29,30} This viewpoint was also the case in Bangladesh, where communities impacted by Nipah virus outbreaks developed causal explanations involving supernatural powers.\textsuperscript{31} This belief may in turn explain why costly interventions are needed to change human practices despite the availability of affordable solutions such as bamboo skirts on trees that prevent bats from accessing and contaminating palm sap.\textsuperscript{14} Similarly, intensive actions may be required in Cambodia because our ethnographic study showed interviewees were only aware of two zoonotic diseases, including avian influenza, for which massive national awareness campaigns have been implemented. As such, our study suggests efforts to improve zoonotic risk awareness in general may be needed before specific communication programmes are planned. Our findings also suggest that interventions related to the risk of Nipah emergence should focus on hunting and consumption of fruit bats, consumption of fruit partially eaten by animals, palm-nectar collection practices and dissociation of pig farming and fruit farming.

In conclusion, our integrated approach allowed us to gather information on different components of a complex socio-ecosystem where Nipah virus could emerge. Although each study provides insufficient information to draw any conclusions, when considered together, recommendations can be provided to interrupt potential transmission routes and limit the risk of disease emergence.
As bats are hosts of major zoonotic pathogens, such studies would likely also help to reduce the risk of emergence of other bat-borne diseases, including diseases similar to severe acute respiratory syndrome or COVID-19.\textsuperscript{32,33} While the precise chain of events leading to the emergence of severe acute respiratory syndrome coronavirus-2 and its precise origin are still unknown, studies suggest the virus originated in bats.\textsuperscript{1,34} Integrated approaches are necessary to better understand the factors driving these emergences and implement efficient and socially acceptable surveillance and control measures at the interfaces between bats and humans. In this context, the emergence of COVID-19 should act as a reminder that stringent efforts will be required to reduce the risk of future pandemics.

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**Competing interests:**

PB is an employee of GSK Vaccines.

**References**


Table 1. Main results of the knowledge, attitude and practice study in two provinces, Cambodia, 2016

<table>
<thead>
<tr>
<th>Variable</th>
<th>No. (%) of respondents</th>
<th>Battambang province (n = 254 from 103 households)</th>
<th>Kandal province (n = 205 from 77 households)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Frequency of consuming palm juice</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Never</td>
<td>118 (46.4)</td>
<td>56 (27.3)</td>
<td></td>
</tr>
<tr>
<td>Occasionally</td>
<td>117 (46.1)</td>
<td>114 (55.6)</td>
<td></td>
</tr>
<tr>
<td>Often</td>
<td>15 (5.9)</td>
<td>19 (9.3)</td>
<td></td>
</tr>
<tr>
<td>Very often</td>
<td>4 (1.6)</td>
<td>16 (7.8)</td>
<td></td>
</tr>
<tr>
<td><strong>Type of palm juice consumed</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Raw</td>
<td>131 (51.6)</td>
<td>84 (41.0)</td>
<td></td>
</tr>
<tr>
<td>Processed</td>
<td>14 (5.5)</td>
<td>67 (32.7)</td>
<td></td>
</tr>
<tr>
<td>Don’t know</td>
<td>109 (42.9)</td>
<td>43 (21.0)a</td>
<td></td>
</tr>
<tr>
<td><strong>Frequency of hunting fruit bats</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Never</td>
<td>210 (82.7)</td>
<td>186 (90.7)</td>
<td></td>
</tr>
<tr>
<td>Occasionally</td>
<td>34 (13.4)</td>
<td>17 (8.3)</td>
<td></td>
</tr>
<tr>
<td>Often</td>
<td>8 (3.1)</td>
<td>2 (1.0)</td>
<td></td>
</tr>
<tr>
<td>Very often</td>
<td>2 (0.8)</td>
<td>0 (0.0)</td>
<td></td>
</tr>
<tr>
<td><strong>Frequency of consuming fruit bats</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Never</td>
<td>227 (89.4)</td>
<td>173 (84.4)</td>
<td></td>
</tr>
<tr>
<td>Occasionally</td>
<td>22 (8.6)</td>
<td>29 (14.1)</td>
<td></td>
</tr>
<tr>
<td>Often</td>
<td>2 (0.8)</td>
<td>2 (1.0)</td>
<td></td>
</tr>
<tr>
<td>Very often</td>
<td>3 (1.2)</td>
<td>1 (0.5)</td>
<td></td>
</tr>
<tr>
<td><strong>Use of partially eaten fruit by households</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eat fruit</td>
<td>11 (10.7)</td>
<td>5 (6.5)</td>
<td></td>
</tr>
<tr>
<td>Feed animals</td>
<td>9 (8.7)</td>
<td>15 (19.5)</td>
<td></td>
</tr>
<tr>
<td>Cook</td>
<td>0 (0.0)</td>
<td>12 (15.6)</td>
<td></td>
</tr>
<tr>
<td>Nothing or thrown away</td>
<td>76 (73.8)</td>
<td>37 (48.1)</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>7 (6.8)</td>
<td>8 (10.3)</td>
<td></td>
</tr>
<tr>
<td><strong>Can fruit bats transmit diseases to humans?</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yes</td>
<td>NA</td>
<td>3 (7.3)</td>
<td></td>
</tr>
<tr>
<td>No</td>
<td>NA</td>
<td>13 (31.7)</td>
<td></td>
</tr>
<tr>
<td>Don’t know</td>
<td>NA</td>
<td>25 (61.0)</td>
<td></td>
</tr>
</tbody>
</table>

NA: not applicable.

a Only 194 respondents replied to this question.

b Only one respondent per household replied to this question.

c Only 41 respondents from Kandal province replied to this question.

Notes: Surveys were conducted in Kandal in April to September 2016 and in Battambang in July 2016. Palm juice was most commonly consumed in raw form. While most respondents disposed of partially eaten fruits, practices including consumption or feeding them to animals were still relatively common.18
Fig. 1. Location of study sites in Cambodia and studies undertaken at each site, 2013–2016

GPS: global positioning system; KAP: knowledge, attitude and practice.
Fig. 2. Population dynamics and reproductive phenology of *Pteropus lylei* in Kandal province, Cambodia, 2013–2016

Notes: Light shading indicates pregnancy periods (December to March) and darker shading indicates lactation periods (April and May).
Fig. 3. Percentage of plant species in faecal samples from *Pteropus lylei* in Kandal province, Cambodia, 2014

Notes: We analysed a total of 210 faecal samples collected from December 2013 to May 2014.
Fig. 4. Percentage of Nipah virus-positive samples from individual sampling sessions of *Pteropus lylei* urine in Kandal province, Cambodia, 2013–2016

CI: confidence interval.

Notes: We collected a total of 3157 urine sample (range: 39 to 156 samples per session). Circles show the percentage of samples that were Nipah virus-positive at each session and bars show 95% confidence intervals. Light shading indicates pregnancy periods (December to March) and darker shading indicates lactation periods (April and May).