

Original Contribution

Bats Without Borders: Long-Distance Movements and Implications for Disease Risk Management

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Abstract: Fruit bats of the genus *Pteropus* (commonly known as flying-foxes) are the natural hosts of several recently emerged zoonotic viruses of animal and human health significance in Australia and Asia, including Hendra and Nipah viruses. Satellite telemetry was used on nine flying-foxes of three species (*Pteropus alecto* $n = 5$, *P. vampyrus* $n = 2$, and *P. neohibernicus* $n = 2$) to determine the scale and pattern of their long-distance movements and their potential to transfer these viruses between countries in the region. The animals were captured and released from six different locations in Australia, Papua New Guinea, Indonesia, and Timor-Leste. Their movements were recorded for a median of 120 (range, 47–342) days with a median total distance travelled of 393 (range, 76–3011) km per individual. *Pteropus alecto* individuals were observed to move between Australia and Papua New Guinea (Western Province) on four occasions, between Papua New Guinea (Western Province) and Indonesia (Papua) on ten occasions, and to traverse Torres Strait on two occasions. *Pteropus vampyrus* was observed to move between Timor-Leste and Indonesia (West Timor) on one occasion. These findings expand upon the current literature on the potential for transfer of zoonotic viruses by flying-foxes between countries and have implications for disease risk management and for the conservation management of flying-fox populations in Australia, New Guinea, and the Lesser Sunda Islands.

Keywords: *Pteropus*, fruit bat, flying-fox, satellite telemetry, Nipah virus, Hendra virus

INTRODUCTION

Bats have been identified as reservoir hosts for numerous recently emerged pathogens that threaten livestock and human health, including Hendra virus (Halpin et al., 2000), Nipah virus (Johara et al., 2001), SARS coronavirus (Li et al., 2005), Ebola virus (Leroy et al., 2005), Australian bat lyssavirus (Fraser et al., 1996), and Menangle virus (Philbey

et al., 2008). A number of these viral pathogens have had significant health and economic impacts, e.g., Nipah virus, Ebola virus, and SARS coronavirus (Calisher et al., 2006).

Knowledge of the distribution and movement patterns of species that act as the reservoir hosts of emerging viruses is necessary to determine the connectivity between host populations and thus identify regions at risk of disease emergence. This information also predicates an understanding of the spatial dynamics of infection among host populations and contributes to risk assessment and disease

management. The risk of disease posed by geographic translocation of bats has been reviewed (Constantine, 2003) with many cited examples of natural and anthropogenic movement of bats found to be infected with potentially fatal zoonotic pathogens.

Fruit bats of the genus *Pteropus* (commonly known as flying-foxes) tend to roost in large camps, almost always in trees, and feed primarily on fruit and flowers. Several species have very large geographical ranges and may exhibit partially migratory or nomadic lifestyles with food availability likely to be the most significant factor driving movement patterns (Fleming and Eby, 2003). Previous studies of the long-distance movement of flying-foxes have used radiotelemetry and banding techniques. However, these approaches have limited application due to the spatial scale involved. Satellite telemetry has the potential to overcome this limitation and has been utilized to track a small number of individuals of *Pteropus poliocephalus*, *Pteropus vampyrus*, and *Eidolon helvum* (Tidemann and Nelson, 2004; Richter and Cumming, 2008; Epstein et al., 2009).

The newly recognized Hendra virus and Nipah virus (genus *Henipavirus*; family *Paramyxoviridae*) seem to be largely confined to the genus *Pteropus*, with Hendra virus isolated from *P. alecto* and *P. poliocephalus* in Australia (Halpin et al., 2000), and Nipah virus isolated from *P. vampyrus* and *P. hypomelanus* in Malaysia (Chua et al., 2002; Sharifah et al., 2009) and *P. lylei* in Cambodia (Reynes et al., 2005). Nipah virus also has been detected by PCR in *P. lylei* from Thailand (Wacharapluesadee et al., 2005) and evidence of exposure to henipaviruses or related viruses has been reported from bats in Indonesia (Sendow et al., 2009), China (Li et al., 2008), Bangladesh (Hsu et al., 2004), India (Epstein et al., 2008), Madagascar (Iehle et al., 2007), and Ghana (Hayman et al., 2008). The potential for overlap in distribution of Hendra and Nipah viruses and for flying-foxes to act as vectors for long-distance transmission of these viruses is largely unknown. Nipah virus, which (in Bangladesh) has transmitted directly from human to human, appears to pose a greater threat to human populations than Hendra virus because it has been responsible for many more human deaths, and has so far had much greater economic impact (Field et al., 2007; Wacharapluesadee et al. 2009).

Elucidation of the interface or divide between these two viruses and their respective hosts is the impetus for this study. We will address the following questions: (1) What is the scale of the long-distance movements of three large

Pteropus species (*P. alecto*, *P. vampyrus*, and *P. neohibernicus*) in northern Australia, New Guinea, and the Lesser Sunda Islands? and (2) Is there connectivity of bat populations between Australia, New Guinea, and the Lesser Sunda Islands that could allow the transmission of viral zoonoses across these regions?

We placed satellite transmitters on two *P. vampyrus* in Timor-Leste, two *P. neohibernicus* in Papua New Guinea, and five *P. alecto* in northern Australia, southern New Guinea, and Sumba, Indonesia and subsequently determined their long-distance movements.

METHODS

Flying-foxes were caught in six locations that were either roosting or feeding sites, fitted with transmitters, and released. They were caught in mist nets set at identified roosting and feeding sites and anesthetized for attachment of the transmitter and collar. Inhalation anesthesia, delivering isoflurane (Isoflurane, Laser Animal Health Pty Limited) and oxygen via an anesthetic machine, was used in Australia (Bats A–C) following the protocol described by (Jonsson et al., 2004). In Timor-Leste, Papua New Guinea, and Indonesia (Bats D–I), flying-foxes were anesthetized using a combination of ketamine (Ketamil, Ilium, Smithfield, Australia) and medetomidine (Domitor, Novartis, Pendle Hill, Australia) injected into the pectoral muscles at similar doses to those stated by Middleton et al. (2007). Atipamezole was used to reverse the effects of medetomidine.

Animal suitability for telemetry was determined by physical examination on the basis of being in good health (free from any signs of disease or abnormalities), body condition, and of sufficient size such that the combined weight of transmitter and collar were <3% of bodyweight (Bander and Cochran 1991).

Four models of platform transmitter terminals (PTTs) produced by Microwave Telemetry Inc. (Columbia, USA) were used: 12- and 18-g solar-powered PTTs, and 20- and 22-g battery-powered PTTs (Table 1) as described by Epstein et al. (2009). Location data were received from the Argos processing centre using Telnet Client and Telnet Inferno (Microsoft, United States) or received by email from the Argos Automatic Distribution Service. The data were imported into, and plotted on, Arcview 3.3 (Environmental Research Systems Institute, Inc, United States) using Argos Tools (GIS-Lab, Russia, <http://gis-lab.info/programs/argos>). Transmitter duty cycles were set for transmission periods of

Table 1. Details of individual flying-foxes on which transmitters were placed and their recorded movements

Bat	Species	Bodyweight (g)	Sex	Location captured and released (see Fig. 1)	PTT model	Duty cycle on/off hours	Days active	Total distance travelled (km)	Mean distance travelled per 7 days (km)	Maximum radial distance from release site (km)
A	<i>P. alecto</i>	650	Male	Coen Australia	18 g solar	12/155	121	508	29.4	139.1
B	<i>P. alecto</i>	650	Male	Thursday Island Australia	18 g solar	12/155	231	393	11.9	46.6
C	<i>P. alecto</i>	600	Male	Thursday Island Australia	18 g solar	12/155	225	1653	51.4	175.9
D	<i>P. alecto</i>	480	Male	Wasi Kussa River Papua New Guinea	12 g solar	7/155	342	3011	61.6	248.6
E	<i>P. alecto</i>	450	Male	Sumba Indonesia	12 g solar	7/155	47	105	15.6	36.5
F	<i>P. neohibernicus</i>	1107	Female	Wasi Kussa River Papua New Guinea	22 g battery	8/120	120	960	56.0	73.1
G	<i>P. neohibernicus</i>	1030	Male	Fly River Delta Papua New Guinea	22 g battery	8/120	62	255	28.8	31.2
H	<i>P. vampyrus</i>	840	Male	Suai Timor-Leste	20 g battery	7/155	47	76	11.3	17.5
I	<i>P. vampyrus</i>	974	Male	Suai Timor-Leste	20 g battery	7/155	47	126	18.8	56.0

7–12 h every 120–155 h depending on PTT model. One location fix comprised of latitude, longitude, time of transmission, and accuracy of location data (Error Class). Individual fixes were assigned to one of seven error classes by Argos; fixes falling in the most accurate four error classes were used in this study. This follows the approach of Tidemann and Nelson (2004) and Epstein et al. (2009), tracking the long-distance movements of flying-foxes in Australia and Asia.

The habitat usage of the bats following release was determined predominantly using Google Earth (Sheppard and Cizek, 2009) and ground truthing when possible on subsequent field surveys to the areas concerned.

The studies performed on live animals followed American Society of Mammals guidelines (Gannon and Sikes 2007) and were approved by the Queensland Department of Industries and Fisheries and The University of Queensland animal ethics committees, the Queensland Parks and Wildlife Service, and respective wildlife agencies in Papua New Guinea, Indonesia, and Timor-Leste.

RESULTS

Transmitters were placed on nine adult flying-foxes from three species: five *Pteropus alecto* (northern Australia ($n = 3$), southern Papua New Guinea ($n = 1$), and Sumba, Indonesia ($n = 1$)), two *P. vampyrus* (Timor-Leste), and two *P. neohibernicus* (Papua New Guinea). Figure 1 shows the capture and release locations of these bats and the species' distributions. Their movements were tracked for a total of 170 (range, 7–49) weeks (Table 1). Individual bat transmission records ranged from 47 to 342 (median, 120) days, and total distance travelled ranged from 76 to 3011 (median, 393) km.

Bat A

On June 9, 2003, a transmitter was placed on a 650-g adult male *P. alecto* near Coen, far north Queensland. During active transmission for 121 days, the bat travelled a recorded maximum radial distance of 139 km from the release site with a total recorded distance travelled of 508 km. This animal traversed Cape York Peninsula from the east coast, 189 km west, to within 37 km of the west coast of the peninsula and predominantly utilized undisturbed tropical savannah habitat but also was recorded in riparian forest and coastal mangroves.

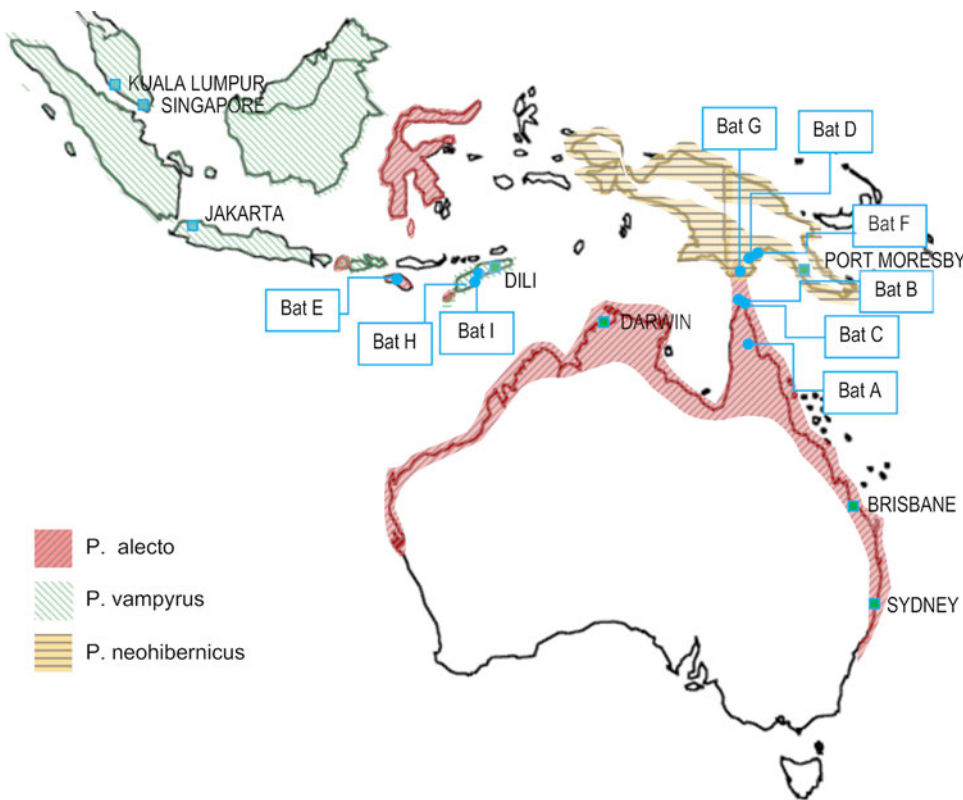


Fig. 1. Distribution of *Pteropus alecto*, *P. vampyrus*, and *P. neohibernicus* in the study region. Locations of release of satellite collared bats is indicated.

Bat B

On October 17, 2003, a transmitter was placed on a 650-g adult male *P. alecto* on Thursday Island, Torres Strait. The transmitter was active for 231 days, during which time the bat travelled a recorded maximum radial distance of 46 km from the release site with a total recorded distance travelled of 393 km. Movements took place among four islands in the southernmost part of Torres Strait and this bat utilized savannah, wet forest, and mangrove habitats as well as urban areas.

Bat C

On October 18, 2003, a transmitter was deployed on a 600-g adult male *P. alecto* on Thursday Island, Torres Strait (Fig. 3). The transmitter was active for 225 days; the bat travelled a recorded maximum radial distance of 175 km from the release site with a total recorded distance travelled of 1653 km. This animal crossed Torres Strait from south to north over 150 km of open sea. It then spent at least 14 days on mainland Papua New Guinea in mangrove and riparian forest habitat before returning to Thursday Island from where it made excursions further south, including over mainland Australia. As with bat B, this animal utilized

savannah, wet forest, and urban areas when on Torres Strait islands.

Bat D

On July 18, 2006, a transmitter was deployed on a 480-g adult male *P. alecto* on the Wasi Kussa River in Western Province, Papua New Guinea (Fig. 3). The transmitter was active for 342 days, during which time the bat travelled a recorded maximum radial distance of 248 km from the release site with a total recorded distance travelled of 3011 km. This animal moved from inland Papua New Guinea, south to Aubusi Island, Australia, in northern Torres Strait. It then returned to mainland Papua New Guinea and travelled over 300 km in a north-westerly direction into Indonesian Papua. During the next 267 days, it moved between Indonesian Papua and Papua New Guinea on nine further occasions. The animal utilized predominantly savannah and riparian habitats, although it also was recorded in urban and cultivated areas in Indonesia.

Bat E

On August 29, 2007, a transmitter was deployed on a 450-g adult male *P. alecto* on the island of Sumba, Indonesia. The

transmitter was active for 47 days; the bat travelled a recorded maximum radial distance of 36 km from the release site with a total recorded distance travelled of 105 km. This animal utilized predominantly deciduous monsoon forest and cultivated areas on Sumba but also spent some time in lowland evergreen forest.

Bat F

On July 17, 2006, a transmitter was deployed on a 1107-g adult female *P. neohibernicus* near Sibidiri on the Wasi Kussa River, Western Province, Papua New Guinea (Fig. 3). The transmitter was active for 120 days; the bat travelled a recorded maximum radial distance of 73 km from the release site with a total recorded distance travelled of 960 km. This animal's movements were confined to the savannah and riparian habitat of the TransFly region of Western Province, Papua New Guinea.

Bat G

On July 21, 2006, a transmitter was deployed on a 1030-g adult male *P. neohibernicus* at Sewerimabu on the Fly River, Western Province, Papua New Guinea (Figs. 2, 3). The



Fig. 2. An adult male *Pteropus neohibernicus* (Bat G) fitted with a 22-g battery-powered satellite transmitter immediately before release in Papua New Guinea.

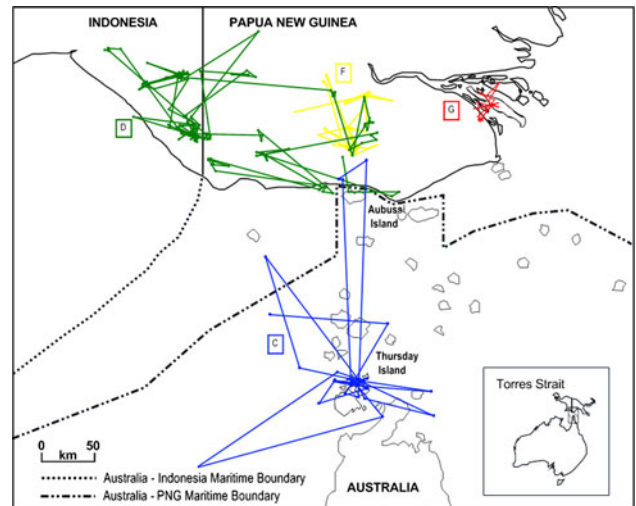


Fig. 3. Movements of bats C, D, F, and G in Torres Strait and southern New Guinea.

transmitter was active for 62 days; the bat travelled a recorded maximum radial distance of 31 km from the release site with a total recorded distance travelled of 255 km. This animal remained in mangrove forest and moved among five islands within the Fly River Delta and the southern bank of the river.

Bat H

On December 12, 2005, a transmitter was deployed on an 840-g adult male *P. vampyrus* near Suai, Timor-Leste. The transmitter was active for 47 days, during which time the bat travelled a recorded maximum radial distance of 17 km from the release site with a total recorded distance travelled of 76 km. This animal's movements were confined to the relatively heavily populated southwest corner of Timor-Leste with all day-time (roosting) fixes located in coastal mangrove areas, whereas nighttime fixes indicated foraging occurring several kilometers inland, including among cultivated areas of fruit and palm trees.

Bat I

On December 19, 2005, a transmitter was deployed on a 974-g adult male *P. vampyrus* near Suai, Timor-Leste. The transmitter was active for 47 days; the bat travelled a recorded maximum radial distance of 56 km from the release site with a total recorded distance travelled of 126 km. This animal travelled in a south-westerly direction into West Timor, Indonesia, where it showed similar roosting and foraging patterns to bat H in Timor-Leste.

DISCUSSION

This study is the first to record by satellite telemetry the long-distance movements of *P. alecto* and *P. neohibernicus* individuals. It also is the first to demonstrate the movement of a flying-fox across Torres Strait between Australia and New Guinea (bat C) and to report the presence of *P. alecto* in the Papua province of Indonesia (bat D) (Helgen 2007). Our study is concordant with observations by Eby (1991), Tidemann and Nelson (2004), and Epstein et al. (2009) that members of the *Pteropus* genus are able to travel very long distances, with one of the *P. alecto* individuals (bat D) that we tracked travelling more than 3,000 km during an 11-month period. The study also has recorded several movements of flying-foxes across national boundaries, indicating the potential for transmission of pathogens between countries. A comparable situation has been recently documented in Africa with the long-distance movement and potential for disease transmission by the straw-colored fruit bat (*E. helvum*) between Zambia and the Democratic Republic of Congo (see Richter and Cumming, 2008).

Design limitations inherent in most telemetry studies mean that generalization of findings of the few studied individuals to populations as a whole need to be made with care. In this study, animals were nonrandomly selected and individuals were captured and released at different times of year with only three of nine being monitored for more than 6 months. Nevertheless, the results show that considerable distances can be travelled by at least some individuals in the population and are relevant to both wildlife management and animal and public health authorities.

Richter and Cumming (2008) highlight the importance of transmitter weight in telemetry studies of bats with the transmitters in their study constituting 3.1–4.0% (mean 3.7%; $n = 4$) of the animal's bodyweight. The transmitters used in the present study constituted a smaller proportion of bodyweight at 2.0–3.0% (mean 2.5%; $n = 9$), hence reducing potential effects on behavior of the bats. The particularly large size of flying-foxes and their tendency to fly above the forest canopy make them suitable candidates among bats for the application of satellite telemetry technology.

Pteropus alecto (Bats A–E)

The data from bats C and D illustrate the ability of individuals of this species to undertake movements of hundreds of kilometers, including the traversing of significant distances over sea. *Pteropus alecto* has not previously been

reported to make long-distance movements and, as a dietary generalist, it has been suggested that this species may be more sedentary than *P. poliocephalus* and *P. scapulatus*, which are primarily nectarivorous and follow seasonal pulses of nectar (Parry-Jones and Augee, 1992; Markus and Hall, 2004). A 12-month radiotelemetry study of *P. alecto* in northern Australia by Palmer and Woinarski (1999) showed a maximum roost-to-roost movement of 133 km, with a mean of 35 km; Woinarski et al. (2007) reported an approximate 25 km crossing over sea from mainland Australia to Melville and Bathurst Islands for this species. However, a genetic study of *P. alecto* in eastern and northern Australia, using allozyme electrophoresis, has indicated a high level of gene flow among populations, suggesting long-distance movements may indeed occur among populations within Australia (Webb and Tidemann, 1996).

P. alecto is known to occur in northern Cape York Peninsula and Torres Strait islands, but has only been recorded on mainland New Guinea on two previous occasions, in 1937 (Tate, 1942) and 1973 (Waithman, 1979). The limited historical records of *P. alecto* on mainland New Guinea may reflect a lack of previous survey effort, a recent northern expansion of the range, or an increased abundance of this species in the area. Consistent with the latter interpretation is the finding that *P. alecto* has expanded its range southwards along the east coast of Australia, from the Mary River in the 1930s (Ratcliffe, 1932) to Sydney in 2007 (Parry-Jones, 2007), a distance of more than 950 km.

P. neohibernicus (Bats F and G)

Little is known of the movement patterns of *P. neohibernicus*, but it has been observed to form large camps in swamp forest and forage in rainforest in nearby hills in Papua New Guinea (Flannery, 1995). It has been recorded feeding during the day and also flying over the sea to pluck floating fruits from the surface (Bonaccorso, 1998). In the present study, the movement patterns have shown this species forages among islands in the Fly River delta with a radius of 73 and 31 km covered by bats F and G respectively, less than some *P. alecto* (139, 175, and 248 km radii for bats A, C, and D, respectively). One *P. neohibernicus* (bat G) and one *P. alecto* (bat D), which were captured at the same roost and released within a few days of each other showed very different movement patterns, with bat G remaining in Papua New Guinea while bat D moved to

Australian Torres Strait islands and also to Papua, Indonesia (Fig. 3). This is consistent with the fact that *P. neohibernicus* has never been reported from Australia, including the Torres Strait islands, although it occurs on mainland New Guinea immediately north of this area.

P. vampyrus (Bats H and I)

It has been suggested that *Pteropus vampyrus* is comprised of five subspecies (Simmons, 2005). However, genetic studies, incorporating all claimed subspecies, do not show differentiation, thus suggesting high levels of gene flow between populations in peninsular Malaysia, Sumatra, Java, Borneo, and the Lesser Sunda Islands (Olival, 2008). Individuals of this species have been recorded travelling up to 50 km per night and flying short distances between islands to forage (Mickleburgh et al., 1992). In the present study, *P. vampyrus* yielded the least data of the three species monitored in terms of duration of transmission, with a combined total of only 94 days of movements being recorded. Bat I moved from Timor-Leste to Indonesian West Timor, and both individuals showed foraging activity in areas of cultivated plants and human settlements. The apparent limited mobility of these bats is at odds with other studies (below), and it is possible that our findings are confounded by the limited duration of transmission, which may have precluded seasonal or biological pressures that induce greater distance movement. Satellite telemetry has previously been used to track the movements of *P. vampyrus* in peninsular Malaysia and Sumatra with four animals travelling across approximately 50 km of open sea (the Strait of Malacca) from peninsular Malaysia to Sumatra, and later returning to peninsular Malaysia (Daszak et al., 2006; Olival and Higuchi, 2006; Epstein et al., 2009). The movements of three bats, tracked for 84–112 days, and travelling average distances of 26, 30, and 58 km per week (total distances 360, 810, and 420 km) (Olival and Higuchi, 2006) were greater than the distances travelled by *P. vampyrus* in the present study (11 and 19 km per week), and comparable to those of *P. alecto* and *P. neohibernicus*.

DISEASE AND CONSERVATION IMPLICATIONS

The three pteropid species tracked in this study are all known to host Hendra or Nipah viruses. Hendra virus has been isolated from *P. alecto*, and this species is believed to

be one of the reservoirs for this virus (Halpin et al., 2000). Neutralizing antibodies to Hendra virus have been found in *P. neohibernicus* from the north coast of Papua New Guinea (Mackenzie, 1999), and neutralizing antibodies to Nipah virus have been found in *P. vampyrus* on peninsular Malaysia (Johara et al., 2001), Java and Sumatra (Sendow et al., 2006). Thus, each of these pteropid species has the potential to transmit Nipah or Hendra viruses. The frequency and scale of transboundary movements add to the findings of previous studies and further demonstrate the potential for the introduction of henipaviruses and other bat-associated infectious diseases to adjacent populations, and/or indicate the likelihood of this having occurred in the past.

The Torres Strait has been viewed as a putative ecological boundary to animals, humans, and plants (Walker, 1972) with *P. neohibernicus* and *P. macrotis* occurring throughout lowland New Guinea (Papua New Guinea and Indonesia) but not occurring in Australia (Bonaccorso, 1998). Similarly *P. scapulatus* is widespread in northern Australia, including the Torres Strait islands but has only been reported from New Guinea on one occasion (Waithman, 1979). Our study suggests that for *P. alecto*, Torres Strait seems to be readily traversable and that a contiguous population of *P. alecto* may occur from northern Australia, through the TransFly region of Papua New Guinea into southeast Papua, Indonesia. Hence, the flying-foxes in these three areas may share the same pathogens, including henipaviruses and others, such as lyssaviruses and Dengue virus.

Flying-foxes move in response to variable food resources, and their movements do not recognize protected area or national boundaries. They are taxa of high conservation concern; 27 of the 52 *Pteropus* species are considered threatened with extinction, with hunting and habitat loss identified as the main drivers of population declines (IUCN, 2010). The hunting of flying-foxes for food occurs across the area covered by this study and increasingly frequent contact between bats and humans may facilitate disease spillover. The present study shows the potential for close connectivity between flying-fox populations on the Australian and New Guinean land masses, and underscores the importance of consultative cross-border approaches in disease risk management and conservation planning. It also suggests the possibility that *P. alecto* may range more widely than *P. neohibernicus*, highlighting the potential heterogeneity of movement patterns among flying-fox species. A thorough understanding

of flying-fox movement dynamics and the processes that drive them is a necessary prerequisite for mapping the risk of emergence of infectious disease from bats to humans and domestic animals. Assessment of the risk of disease emergence across regions and national boundaries can then meaningfully inform disease surveillance and management strategies, facilitating appropriate and efficient use of limited resources.

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