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Pteropus vampyrus, a hunted migratory species with a multinational home-range and a need for regional management

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Summary

1. The management of migratory species is challenging because of insufficient data on long-range movement patterns, habitat use, and the impact of anthropogenic pressures (e.g. hunting) throughout their home ranges.

2. We evaluate the current abundance and mobility of the Malayan flying fox *Pteropus vampyrus*, a threatened fruit bat species of ecological and economic significance across Southeast Asia, using roost site surveys and satellite telemetry. We combined this with data from hunter license sales and population projection models to assess the impact and sustainability of current hunting practices in Peninsular Malaysia.

3. We monitored 33 active *Pteropus vampyrus* roost sites in Peninsular Malaysia, including eight seasonal roost sites. Roost site occupancy showed considerable temporal variation over the 3-year study period.

4. Hunting activity has more than doubled since 1996, and based on license sales, we estimate that a minimum legal harvest of 87 800 bats occurred between 2002 and 2005. Population models suggest that this level of hunting is likely to be unsustainable given our baseline abundance scenarios of 100 000, 250 000 or 500 000 bats, especially considering that these models do not include culling of Malayan flying foxes as agricultural pests or illegal hunting activities, for which there are no available data.

5. Satellite telemetry of seven adult male bats show that Malayan flying foxes are highly mobile, travelling hundreds of kilometres between roosting sites within a year and occupying home ranges that extend beyond Malaysia to include Indonesia and Thailand. We conclude that focal hunting pressure in Malaysia threatens a regional population of this migratory mammal.

6. *Synthesis and applications*. This is the first study of its kind on flying foxes in Asia, and illustrates that bats, like other migratory species, urgently require comprehensive protection by regional management plans across their range. *P. vampyrus* moves across international borders in Southeast Asia. Current hunting practices within Malaysia together with limited protection in other countries may threaten its long-term survival.

Key-words: abundance, conservation, fruit bat, hunting, large flying fox, Malayan flying fox, migratory, platform terminal transmitter, population survey, *Pteropus vampyrus*, satellite telemetry

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Introduction

Migratory animals present specific management and conservation challenges. These include the need for large protected areas [e.g. ungulates in Africa or North America (Berger 1991; Thirgood *et al*. 2004)]; poor knowledge of movement patterns and habitat use (e.g. sea turtles) (Lopez-Mendilaharsu *et al*. 2005); different pressures on habitat in disparate regions within a species' home range [e.g. neotropical migrant songbirds (Robbins *et al*. 1989; Roca *et al*. 1996)]; and inconsistent protection laws – particularly if a species' home range transcends national boundaries. Some treaties, such as the Convention on Migratory Species (CMS 1979) call for protection of migratory animals throughout their range, but large numbers of migratory species still lack comprehensive protection.

Old World fruit bats of the family Pteropodidae are an ecologically significant group of animals which occupy broad, trans-national home ranges, yet largely lack regional protection as well as baseline population data. These highly mobile frugivorous and nectivorous bats (Eby 1991; Webb & Tidemann 1996) play critical roles in the pollination and seed dispersal of more than 289 commercially and ecologically important plant species, including tropical hardwood trees (Howe & Smallwood 1982; Fujita & Tuttle 1991; Utzurrum 1995; Hodgkison *et al*. 2003). Many pteropodid bats are thought to be in decline (Mickleburgh, Hutson, & Racey 2002), although information about their abundance, habitat utilization or movement patterns is lacking in many cases (Fujita & Tuttle 1991; Mickleburgh *et al*. 2002).

Pteropus species are gregarious, forming roosting colonies of varying size depending on habitat (Pierson & Rainey 1992; Hall & Richards 2000; Kunz & Jones 2000). Australian *Pteropus* spp. are migratory (Fleming & Eby 2003), although detailed movement data for other species are scant. Radiotelemetry studies of Australian *Pteropus* species show that individuals are highly mobile, flying up to 50 km each night to forage (Palmer, Price, & Bach 2000). Australian flying foxes occupy large home ranges, and are generally seasonally nomadic, flying hundreds of kilometres per week as part of their normal movement patterns, usually in response to local food availability (Nelson 1965; Eby 1991; Tidemann *et al*. 1999; Hall & Richards 2000; Kunz & Jones 2000; Palmer *et al*. 2000; Markus & Hall 2004).

Hunting and habitat loss have been identified as the primary threats to pteropodid species throughout their range (Mickleburg, Hutson, & Racey 1992; Mohd-Azlan, Zubaid, & Kunz 2001; Mickleburgh *et al*. 2002). Pteropid bats (of the genus *Pteropus*), in general, have several ecological and biological traits that may make their populations particularly vulnerable to hunting: they aggregate during mating and birthing activities (Hall & Richards 2000), which makes colony sizes larger than usual and hunting is therefore likely to be easier; they are long-lived animals, with relatively long gestation periods (6 months) for their body size (McIlwee & Martin 2002); and they only give birth to one pup per year, which remains dependent on the mother for up to 3 months (Kunz & Jones 2000). Pteropid bats also feed on cultivated fruit, particularly when natural food resources are scarce (Eby 1991) making them an agricultural pest, and providing a justification for hunting.

Pteropid bats are among the largest in the world and are hunted for food, sport or medicine across their ranges (Fujita & Tuttle 1991). The legality of hunting varies by country. For example, in Thailand all four native *Pteropus* species [*P. vampyrus*, *P. hypomelanus*, *P. lylei* and *P. intermedius* (Nowak 1994)] are listed as protected species under the Wild Animal Reservation and Protection Act B.E. 2535, 1992, which prohibits hunting, possession, trade or export. The Forestry Administration in Cambodia also prohibits hunting of *P. vampyrus* (J. Walston, personal communication), while in Indonesia, *Pteropus* spp. are not legally protected, and they are commonly found for sale as food (Lee *et al*. 2005; Struebig *et al*. 2007).

In Malaysia, there are two native pteropid species: *Pteropus vampyrus* (Kunz & Jones 2000), which occurs on the mainland; and *P. hypomelanus* (Jones & Kunz 2000), which inhabits islands around the Peninsula. *Pteropus vampyrus* forms colonies of up to 15 000 individuals (Fujita & Tuttle 1991; Kunz & Jones 2000); however, data on the current population size and the impact of hunting are lacking. The most recent survey of *P. vampyrus* observed 115 locally recognized roost sites on Peninsular Malaysia and found that all but 40 were no longer in use (Mohd-Azlan *et al*. 2001). The authors suggested that a severe population decline had occurred and the known roost sites had been abandoned, although the study included neither population counts nor long-term data on whether 'abandoned' roosts were used seasonally.

On Peninsular Malaysia, hunting pteropid bats is allowed under the Malaysian Protection of Wildlife Act, and hunting licenses are issued by the Department of Wildlife and National Parks (PERHILITAN). In addition to sport hunting, unrestricted culling as agricultural pests (of fruit orchards) is permitted, once clearly specified means have been used to deter the bats. *Pteropus vampyrus* meat is sometimes used medicinally, being considered a remedy for respiratory ailments by the ethnic Chinese Malay community (M. Ho, personal communication). Different hunting laws apply in the two eastern Malaysian states on Borneo: hunting bats is illegal in Sarawak, but bats are not protected in Sabah (http://www.sabah.gov.my/jhl/).

It appears that *P. vampyrus* is more commonly hunted than *P. hypomelanus*, and hunters in Peninsular Malaysia have reported increasing difficulty in locating *P. vampyrus*. Hunting licenses are issued year-round without limit, yet there have been no studies of baseline population sizes or basic behavioural ecology (Fujita & Tuttle 1991; Mohd-Azlan *et al*. 2001) to evaluate the sustainability of this practice.

The objective of this study was to evaluate the status and stability of *P. vampyrus* populations in Peninsular Malaysia by obtaining baseline population estimates, documenting local and long-range movements, and developing dynamic population models from our current understanding of *Pteropus* biology and hunting levels. We use this information to assess the conservation status of *P. vampyrus* in light of current hunting practices and comment on the problems of managing hunted species that migrate over large home ranges.

Materials and methods

ROOST SITE COUNTS

Roost site counts were conducted at irregular intervals between 2003 and 2006 as part of a study of the ecology of Nipah virus, a zoonotic virus carried by *Pteropus* spp. (Epstein *et al.* 2006). Study sites included previously identified roosts (Mohd-Azlan *et al.* 2001) and new sites were identified by interviewing local residents and hunters throughout Peninsular Malaysia. Reported roost sites were visited 2–3 times to verify the continued presence of bats, and if bats were present during the initial and subsequent visit, the site was included in this study and subsequently revisited for counting. Roost sites were considered permanent, if they were occupied by bats at every observation point throughout the study; otherwise, they were considered seasonal or temporary. Roost site counts were conducted by trained field biologists at each colony either during evening fly-out periods (at dusk) or during the day, depending on the accessibility and visibility of the roost site. Fly-out counts were conducted from multiple vantage points when possible, using binoculars and either photography or video recordings (Utzurrum *et al.* 2003). When multiple observers were involved, final roost count estimate was reported as an average. Colony estimates by local contacts were also included, but as a separate data set. GPS coordinates for each colony were recorded using a Magellan Meridian Platinum GPS handheld device (Thales Navigation, Santa Clara, CA, USA). Roost sites reported in this study are shown in Fig. 1.

SATELLITE TELEMETRY

Adult male *P. vampyrus* in good body condition (see Epstein *et al.* 2008) and with a body mass > 700 g were captured using mist nets (Gumal 2004) and were fitted with either 20 g battery-powered platform terminal transmitters (PTT) or 12 g solar-powered PTT (Microwave Telemetry, Columbia, MD, USA). The duty cycle (frequency of activation and duration of signal transmission) varied among PTT as follows: Bats 1–4 carried battery-powered transmitters that switched on and transmitted locations for 12 h every 10 days; Bat 5 carried a solar-powered PTT and transmitted for 7 h every 7 days; Bats 6 and 7 carried a battery-powered PTT and transmitted for 7 h every 5 days. The bats were all released at their capture sites: Bats 1, 5, 6, and 7 at Benut, Johor; Bats 2 and 3 at Lenggong, Perak; and Bat 4 at Kuala Berang, Terengganu, see Fig. 1. Female bats were excluded from this study to avoid adding an extra burden during times of pregnancy and lactation. All transmitters weighed < 3% of the bat's total body mass.

Platform terminal transmitters locations were obtained using the Argos Service (Collecte Localisation Satellites, Ramonville Saint-Agne, France) which categorizes location error into seven classes from least to most error: 3, 2, 1, 0, A, B and Z (CLS 2008). Flight paths were reconstructed using location data with location classes of 3, 2, 1 and 0, which have established error rates, and dismissing location classes A, B and Z, which have no upper limit to their error margins (CLS 2008). Satellite telemetry locations obtained between 06:00 h and 18:00 h were considered roosting sites and locations between 18:00 h and 06:00 h were considered foraging sites. Track and home range location data were imported into ArcView GIS 3·2 (ESRI, Redlands, CA, USA). Tracks were constructed using Argos-tools extension (CLS; America, Inc., Largo, MD, USA). Home range analysis was performed using the Kernel method available in the Home Range Extension for Arcview (Rodgers & Carr 2001). We combined telemetry data from multiple individuals collared at the same site to perform home range analyses, so the resulting ranges can be interpreted as estimates of the frequency distribution of occupation for individuals captured at a given site (Seaman & Powell 1996).

HUNTING DATA

Annual hunting license sales reported by state offices were provided for 2002–2005 by Perhilitan. Monthly license sales and hunter demographic data were provided by state offices only for 2002–2004.

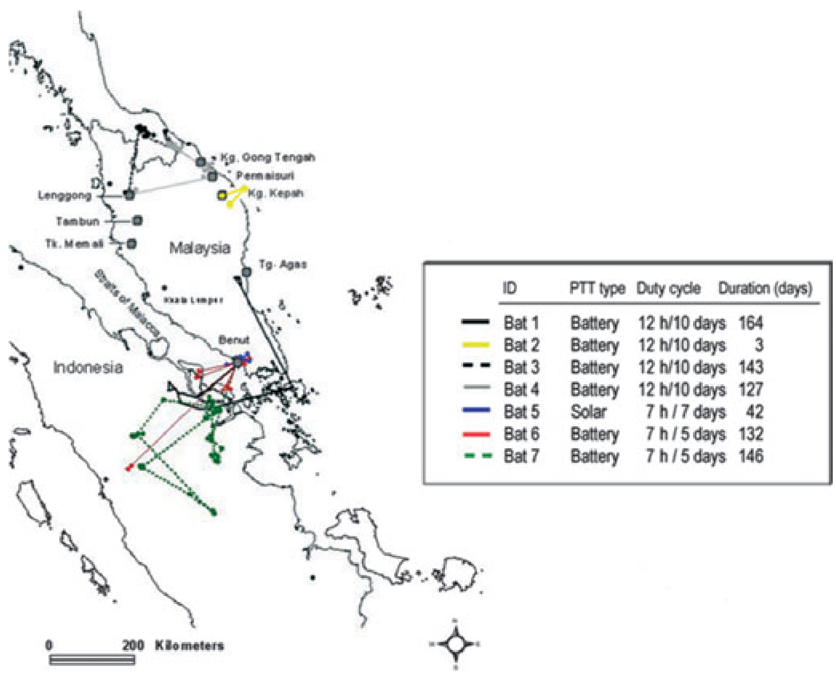

Fig. 1. *Pteropus vampyrus* roost locations used for the population study and the flight paths of seven adult male *P. vampyrus* based on satellite telemetry. The data illustrate that flying foxes are highly mobile and utilize habitat in Malaysia, Indonesia and Thailand.

Hunting licenses are sold by each state and only permit hunting within that state. Hunters must register their permanent residence when applying for a license, but may hold licenses in multiple states. Therefore, to assess hunter mobility, we defined a 'Hunter Index' as:

$$I_H(s) = \frac{L_S}{H_S c};$$

where c is a correction factor for each year and $= L_{\text{tot}}/H_S$ and accounts for the discrepancy between the number of registered hunters in state S (H_s) and the number of licenses issued in that state (L_s) in a given year. A Hunter Index of <1 indicates that hunters are leaving the state to hunt and an index of >1 indicates that non-resident hunters enter the state to hunt.

PTEROPUS VAMPYRUS POPULATION MODELLING

The basic population dynamics of the Malayan flying fox (*Pteropus vampyrus*) were modelled using the following matrix projection model, which describes the numbers of female bats in the population:

$$\vec{N}_{t+1} = M_{\vec{N}} \vec{N}_t \qquad \text{eqn 1}$$

No data are available from which to precisely estimate demographic parameters of wild *P. vampyrus*; however, several natural history observations that appear to be consistent among flying foxes allow us to outline a basic projection model. Female pteropid bats produce at most a single young each year, and reproduction is highly seasonal (Kunz & Jones 2000; McIlwee & Martin 2002). Additionally, female flying foxes in species whose demography has been studied in more detail tend to first successfully rear young at around 3 years of age (McIlwee & Martin 2002). Based on this information, we distinguish four age classes, and

$$\vec{N}_t = \begin{bmatrix} x_t \\ y_t \\ z_t \\ B_t \end{bmatrix} \qquad \text{eqn 2}$$

represents the female population at time t. The first three age classes represent individuals in the first three years of life, respectively, and the fourth age class, denoted $N_{4,t} = B_t$, represents the adult (reproductive) female population. The projection matrix in eqn 1 is defined as

$$M_{\vec{N}} = \begin{bmatrix} 0 & 0 & 0 & f(B_t) \\ s & 0 & 0 & 0 \\ 0 & s & 0 & 0 \\ 0 & 0 & s & s \end{bmatrix} \qquad \text{eqn 3}$$

where $0 < s < 1$ is the annual survival probability (assumed to be constant for individuals of all ages after McIlwee & Martin (2002) and the fertility function, $f(B_t)$, defines the density-dependent reproductive output of the adult age class (reproductive females). We assume age-, sex- and density-independent background mortality, largely because of a lack of evidence to the contrary and a corresponding lack of information to guide alternative assumptions. Given that mortality because of hunting is likely to drastically outweigh other sources of mortality, however, we consider alternative scenarios for the relationship between hunting and population size when hunting is incorporated into the model below.

The documentation of stress-induced abortions in several *Pteropus* species suggests that successful birthing and weaning of offspring may depend on available resources. We assume compensatory (Beverton-Holt) density effects on reproduction and that competition for resources (such as fruit or roosting sites) among adult females determines fertility. Half of the offspring are assumed to be female. The resulting fertility function takes the form

$$f(B_t) = \frac{R}{2(R + B_t)} \qquad \text{eqn 4}$$

where $R > 0$ is a scaling parameter indicating resource availability.

Under this model, the population reaches a stable age distribution and size at

$$\vec{N}* = \begin{bmatrix} x^* \\ y^* \\ z^* \\ B^* \end{bmatrix} = \begin{bmatrix} \frac{R}{2(R+B^*)} \\ \frac{sR}{2(R+B^*)} \\ \frac{s^2R}{2(R+B^*)} \\ s + \frac{s^3R}{2(R+B^*)} \end{bmatrix} B^* \qquad \text{eqn 5}$$

where $B^* = R\left(\frac{s^3-2(1-s)}{2(1-s)}\right)$ is the equilibrium population size of adult females. The equilibrium depends on the annual survival probability s and the overall resource availability (scaled by the parameter $R > 0$), and the population goes extinct (i.e. $B^* \leq 0$) whenever s is less than *c.* 0·77. Assuming that the male annual survival probability is equivalent to the female annual survival probability, the total number of bats in the population at time t is $2\sum \vec{N}_t$

The model can be modified to allow removal of bats by hunting. We assume that there is no age or sex bias in mortality because of hunting. Although this assumption would be violated in the case of many hunted mammals, flying-fox hunting in Peninsular Malaysia primarily consists of shooting flying bats, which suggests that individuals will be equally targeted. The functional form of the hunting response to population size is unknown, and we consider two alternative scenarios: a constant proportion of bats is removed annually; and a constant number of bats is removed annually. The actual response of hunting level to bat population size is likely to be in-between these two scenarios, so these two cases may bound the range of population trajectories that would be expected as a result of realistic hunting practices.

HUNTING MODEL 1: REMOVAL OF A CONSTANT PROPORTION

In case where a constant proportion of the bat population is killed by hunting each year, the annual survival term s is replaced in the projection matrix with the term $(s - h)$, where h is the proportion of the population killed because of hunting each year and $0 < h < s$. The equilibrium size of the adult female population with hunting is

$$B^{*(h)} = R\left(\frac{(s-h)^3 - 2(1-s+h)}{2(1-s+h)}\right), \qquad \text{eqn 6}$$

,and the level of hunting is sustainable when $(s-h)^3 - 2(1-s+h) > 0$. Given our constraints on the values of s and h, hunting is therefore expected to be sustainable (i.e. $B^{*(h)} > 0$) when $(s - h)$ is greater than *c.* 0·77.

HUNTING MODEL 2: REMOVAL OF A CONSTANT NUMBER

In case where a constant number of bats is killed by hunting each year, the form of the equation representing the female bat population (eqn 1) requires modification to include hunting and becomes

$$\vec{N}_{t+1} = M_{\vec{N}} \vec{N}_t - \frac{\vec{H}_t}{2} \qquad \text{eqn 7}$$

where the total number of bats killed annually by hunting H is $\sum \vec{H}_t$(assuming that males and females are killed in equal numbers). We assume that hunting is age-independent so that the number of individuals in an age class killed because of hunting is proportional to the percentage of the total population represented by that age class, giving

$$\vec{H}_t = \begin{cases} \frac{H\left(M_{\vec{N}}\vec{N}_t\right)}{2\sum\left(M_{\vec{N}}\vec{N}_t\right)} & \text{if} \quad \sum\left(M_{\vec{N}}\vec{N}_t\right) \geq \frac{H}{2} \\ M_{\vec{N}}\vec{N}_t & \text{if} \quad 0 \leq \sum\left(M_{\vec{N}}\vec{N}_t\right) < \frac{H}{2} \end{cases} \qquad \text{eqn 9}$$

That is, exactly $\frac{H}{2}$ female bats are removed by hunting annually unless the size of the total female population, $\sum\left(M_{\vec{N}}\vec{N}_t\right)$, is $\leq \frac{H}{2}$, in which case the entire remaining population is removed.

The equilibrium population vector,

$$\vec{N}^{*(H)} = \begin{bmatrix} x^{*(H)} \\ y^{*(H)} \\ z^{*(H)} \\ B^{*(H)} \end{bmatrix} \qquad \text{eqn 10}$$

was determined by model iteration from a starting population at the non-hunted equilibrium for given values of the parameters R and s. Population trajectories were followed for 1000 years (to ensure that equilibrium levels were reached) or until population extinction.

We examined scenarios where the equilibrium population of adult female bats in the absence of hunting, B^*, was 50 000, 125 000 or 250 000 for a range of s values. In Tables S1–S3 (Supporting Information), we show R values corresponding to the given equilibrium adult female populations for each value of s used. We used both extensions of the model to analyse the effect of hunting on the *P. vampyrus* population in Malaysia for a range of h and H values.

Results

SEASONAL DISTRIBUTION AND COLONY ESTIMATES OF *PTEROPUS VAMPYRUS*

Thirty-three *P. vampyrus* roosts were identified and repeatedly surveyed between June 2003 and July 2006 and of those, eight were considered temporary or seasonal (Fig. 1). Roost occupancy fluctuated over time, with the timing of the peak roost counts varying with location (Fig. 2). Our minimum population estimate for *P. vampyrus* in Peninsular Malaysia is the combined maximum count from each of our census sites, 21 600 bats. The largest colony found was in Benut, where up to 6000 bats were counted from a single vantage point during fly-out. Benut consistently had more than 1000 bats during the study period, except on 13 April 2005 when the roost was empty. The smallest *P. vampyrus* roost in our study was at Tambun, at which we counted a maximum of 100 bats.

SATELLITE TELEMETRY

The duration of data transmission from the satellite collars ranged from 3 to 164 days (Fig. 1). The maximum foraging distance recorded was 87·5 (± 1·5) km flown at night between 23:18 h and 04:28 h on 7–8 February 2004 by Bat 1. The maximum distance recorded between two transmissions was Bat 7, which flew 130·0 (± 1·0) km over 2 h between 05:00 h and 07:00 h on 7 December 2005, indicating an average flight speed of 65 km h^{-1}. The maximum distance between two consecutive daytime transmissions (roosting sites) was travelled by Bat 6, which flew 363·4 (± 1·0) km between Benut and Sumatra, recorded 4 days apart. All four satellite-collared bats travelled to Sumatra to forage and roost. Bats 3 and 4, collared in Lenggong, Perak, flew to the same location in Thailand between July and September 2004. The rest of the colony also left Lenggong and bats were not observed there for a period of 16 months. Home range analysis of telemetry data from bats originating in Benut (n = 4) indicates that they spend *c.* 90% of their time within a 128 000 km^2 region that included both Sumatra and Peninsular Malaysia (Fig. 3). Similarly, bats collared in Lenggong (n = 2) appear to spend *c.* 90% of their time in a 64 000 km^2 region that includes Thailand and Malaysia.

HUNTING DATA, PENINSULAR MALAYSIA: 2002–2005

In the period between 2002 and 2006, 1756 *P. vampyrus* hunting licenses were issued by Perhilitan (mean = 440 - $year^{-1}$), permitting a total of 87 800 bats to be killed; about 22 000 per year. This is a minimum estimate, as license data does not account for illegal hunting and unlicensed (but legal) killing of bats to protect fruit crops. Six hundred and thirteen hunters purchased at least one license between 2002 and 2004, and 26% of them purchased multiple licenses. License sales in 2005 (n = 470) were consistent with 2004 (n = 459). Hunting licenses are issued by state, and records for all months were not available from all states. In Fig. 4, state license sales data is presented. Hunting licenses are sold year-round and are valid for 3 months or a maximum take of 50 bats; however, enforcement of limits is minimal. Figure 5 shows the number of hunters living in each state with the number of licenses issued by each state's wildlife office for each year from 2002 to 2004. In 2004, the state of Johor had the highest number of registered hunters in residence (46%; n = 283) followed by Selangor (18%; n = 113) then Perak (10%; n = 62). Johor, Pahang, and Perak had the greatest number of licenses issued in 2004 (38% n = 170; 36% n = 159; and 17% n = 74, respectively). These three states combined issued 90% of all licenses in 2004 (403/446). Hunters may obtain licenses and hunt in states other than where they reside. Table 1 lists the hunter indices for each state for the years 2002–2005. According to their hunter indices, Pahang attracted the most hunters from outside relative to other states until 2005, during which Melaka attracted the most hunters. Perak drew hunters in 2003 and 2004. Selangor, the state that includes Kuala Lumpur, had the lowest (non-zero) hunter index, indicating that while hunters reside there, most leave the state to hunt. Monthly hunting license sales appeared to peak in February–March, and again in July, indicating higher levels of hunting activity during these periods. Bat populations appeared to peak during the months of June and July in several locations, including

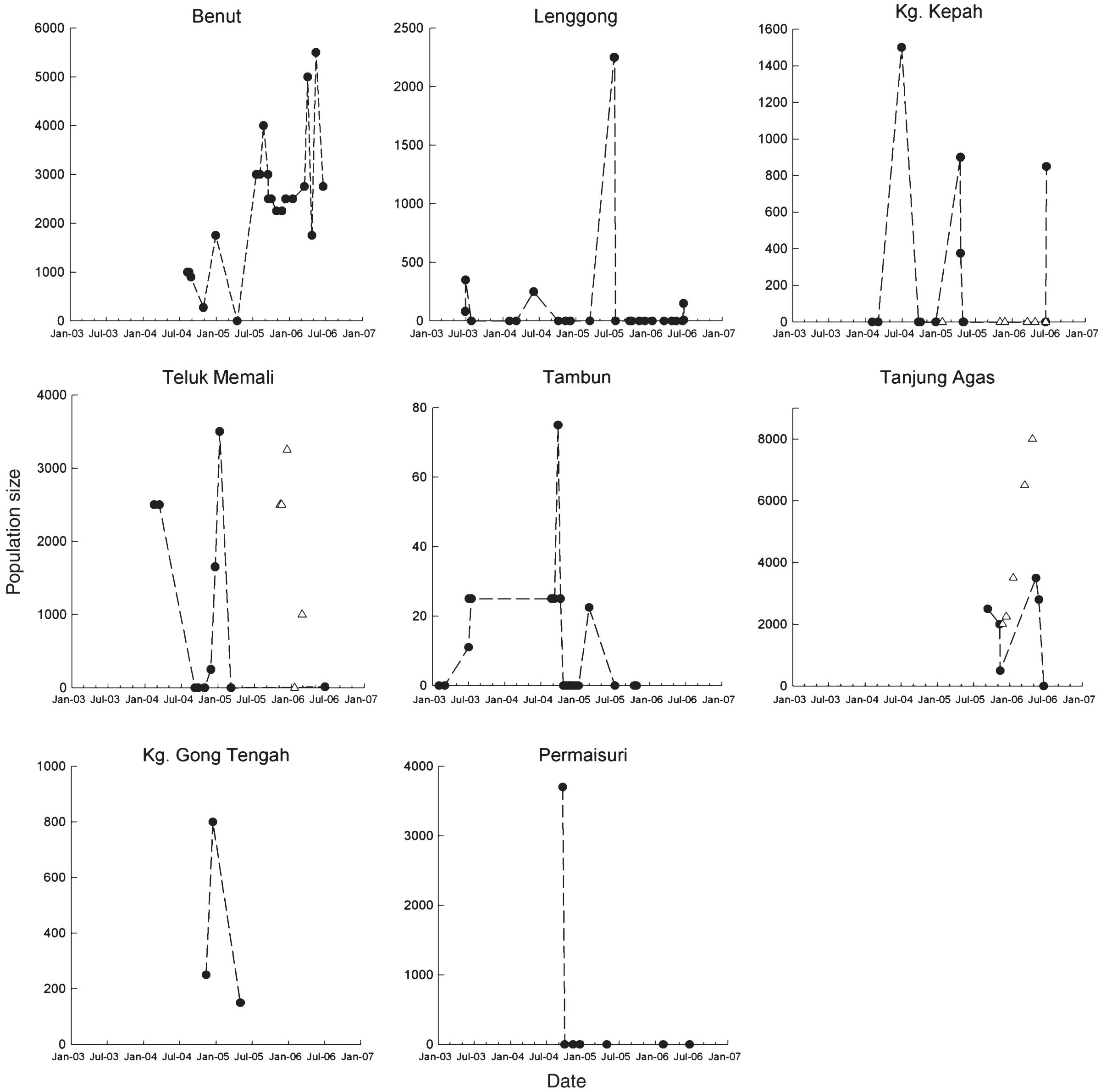

Fig. 2. Colony count estimates reported by trained field personnel (filled circles) and local residents (open triangles) at 8 roosting locations show temporal variation. The time scale is identical for each location, but the vertical axis is adjusted for each site based on the maximum count.

Johor (Benut), Pahang (Tanjung Agas) and Perak (Lenggong). Based on the timing of license sales and license duration, hunting intensity appears to be highest between March and August.

PTEROPUS VAMPYRUS POPULATION MODELLING

For each of the equilibrium adult female population sizes (B^{*}) examined, Table S1 (Supporting Information) indicates the corresponding equilibrium total population size in the absence of hunting ($N^{*} = 2\sum \vec{N}^{*}$). Results of the population projections with hunting are summarized in Figs 6 and 7 and Tables S2 and S3 (Supporting Information) shows the equilibrium total population sizes under each of the hunting scenarios.

HUNTING MODEL 1: REMOVAL OF A CONSTANT PROPORTION

Under the first scenario, in which a constant proportion of the population is hunted, the maximum sustainable yield over all parameter values examined is *c*. 16 000 bats. This level of hunting is sustainable only when the equilibrium population size of the non-hunted population is $>685\,000$ bats and the annual background mortality is very low (10%; $s = 0{\cdot}9$) with an additional mortality from hunting between 4·9% and 6·7% of the population ($h = 0{\cdot}049$–$0{\cdot}067$). The minimum number of bats hunted annually from 2002 to 2005 was *c*. 22 000. If the number of bats hunted annually is a constant proportion of the total bat population, the model suggests that this level of hunting is unsustainable unless the equilibrium size of the non-

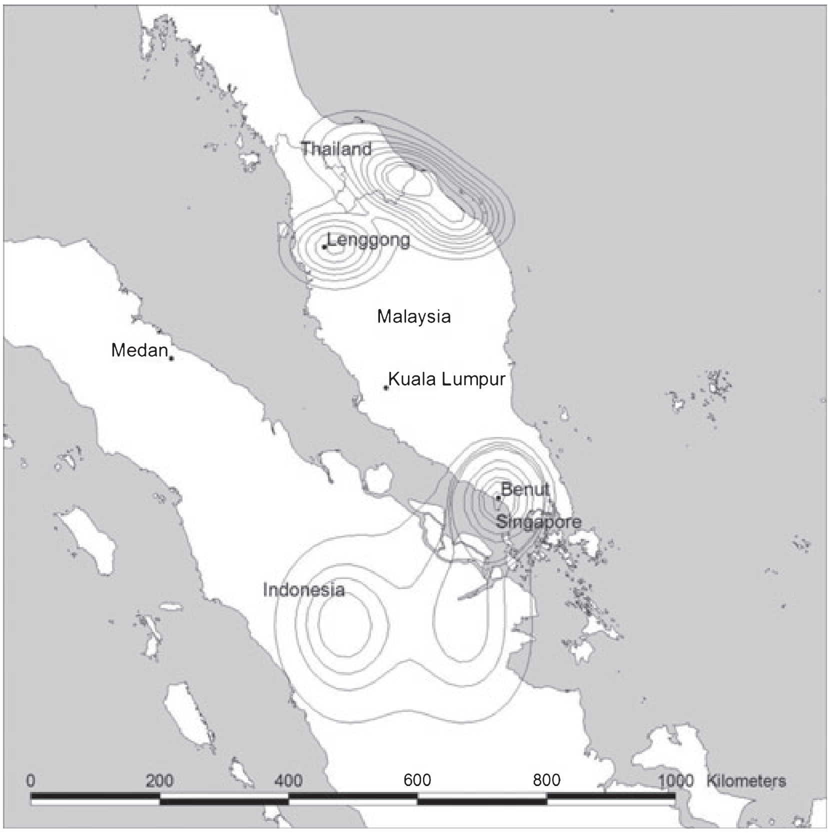

Fig. 3. Home range analysis of seven male *Pteropus vampyrus* based on satellite telemetry data. Bats are expected to spend *c.* 90% of their time within the outermost ring. In the North (n = 3), this includes area in both Malaysia and Thailand and in the South (n = 4) this includes Malaysia, Singapore, and Indonesia (Sumatra). Management strategies for *P. vampyrus* should be coordinated among these countries for optimal conservation.

hunted bat population is substantially higher than the values examined here.

HUNTING MODEL 2: REMOVAL OF A CONSTANT NUMBER

The second model, which assumes that a constant number of individuals are hunted each year, also suggests that an annual yield of 22 000 bats will drive the bat population to extinction for all parameter values and non-hunted equilibrium population sizes examined. Stochasiticity was not explicitly included in this model because of lack of sufficient environmental and population data, however, in general, we believe stochasiticity would decrease the time to extinction. This model predicts extinction within 6–81 years (depending on parameter values) with this level of hunting, assuming that the population starts at the equilibrium population size and age distribution for the non-hunted population (see Table S3, Supporting Information). Lower levels of hunting may be sustainable, particularly if the non-hunted equilibrium is large.

Discussion

In this study, we provide a population survey and quantitative analysis of hunting pressure on *P. vampyrus*, a highly mobile and ecologically important fruit bat species in Malaysia. We also provide evidence that these bats have large home ranges and move frequently across international borders.

POPULATION STATUS AND DISTRIBUTION

We found temporal variation in *P. vampyrus* roost occupation and abundance, supporting previous observations in Borneo that individuals of *P. vampyrus* use multiple roost sites (Gumal 2004); and consistent with habitat use studies of mega and microchiroptera in Madagascar (Kofoky *et al*. 2007). Benut was the most consistently occupied roost site, possibly because of its location in a mangrove swamp which sheltered it from direct hunting disturbance. Our estimated minimum population of 21 600 *P. vampyrus* in Peninsular Malaysia is less than the reported licensed hunting allowance. It is likely that there are either additional, unobserved active roost sites or substantial bat movement between Malaysia and Thailand or Sumatra. The former explanation is possible, as some national parks were inaccessible during our multi-year study, though other surveys of these regions did not report bat colonies. The observations that all four bats collared and released in Benut crossed the Straits of Malacca from Malaysia to Sumatra, and that both bats in Perak moved into Thailand suggest that international migration is part of the normal movement patterns of *P. vampyrus*. In fact, our home range analyses suggest that bats spend significant amounts of time foraging and roosting outside of Malaysia. Bat 5 spent four of 4 months in Malaysia and three in Sumatra, further suggesting that bats in these three nations constitute a single population for management purposes. Our telemetry data also suggest that intermediate roosting locations are used during long-distance migratory movements of several hundred of kilometres, emphasizing a

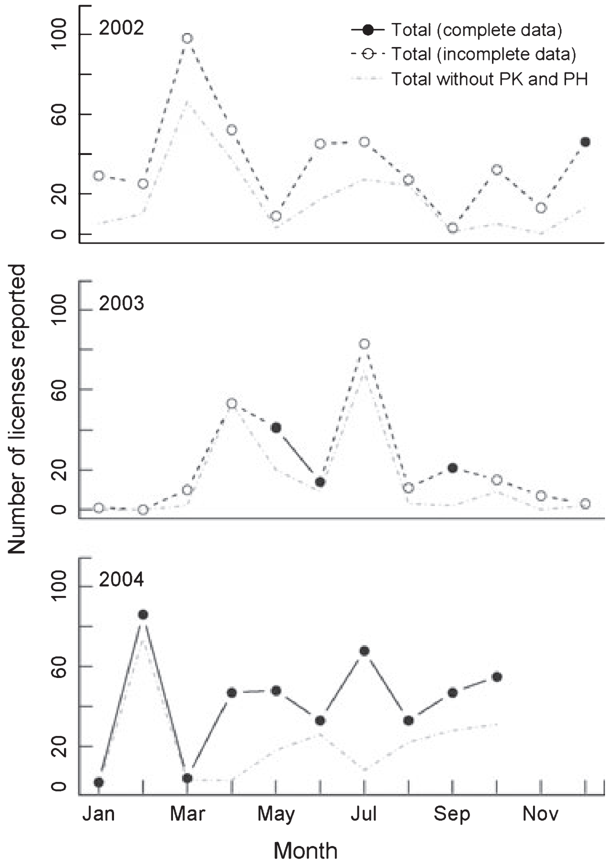

Fig. 4. Monthly reported hunting license sales for 2002 – 2004 in Peninsular Malaysia. Licenses are issued by state, though some records were incomplete. Solid circles and lines denote months with full reporting. Open circles connected by dashed lines indicate months with a single state failing to report licensing data; these points therefore represent a lower bound for the number of licenses issued. Based on the timing of license sales and license duration, hunting intensity appears to be highest between March and August, coinciding with the birthing period of *Pteropus vampyrus* (March/April (Kunz & Jones 2000)). Missing data in 2002 are from Perak, and in 2004 are from Pahang. Reported license totals from all states except Perak and Pahang are also indicated (dashed grey line) to facilitate inter-annual comparison.

Table 1. The 'Hunter Index', reflects the requirement that hunters register in their home state as well as in states where they hunt

Hunter Index by state: 2002–2005				
State	2002	2003	2004	2005
Johor	0·92	0·84	0·82	1·66
Kedah	0·00	0·91	0·68	∞
Kelantan	0·00	0·00	0·00	0·00
Melaka	0·54	0·50	0·27	10·39
Negeri Sembilan	0·21	0·69	0·49	1·14
Pahang	6·46	4·78*	4·73	0·60
Penang	0·00	0·00	0·00	∞
Perak	0·28†	1·47	1·63	0·91
Perlis	0·00	0·00	0·00	0·00
Selangor	0·03	0·05	0·05	N/A
Terengganu	0·51	0·86	1·21	3·15

$I_H(s) = \frac{L_S}{H_{S}c}$; where $c = L_{\mathrm{tot}}/H_S$ is a correction factor to account for a discrepancy between the number of registered hunters in state S (H_s) and the number of licenses issued in that state (L_s) in a given year. The data supports the hypothesis that hunters travel outside their home state to hunt, which creates increased pressure on certain bat populations. A value < 1 indicates that hunters are leaving the state to hunt and > 1 indicates that non-resident hunters are entering the state to hunt. This analysis is based on data that shows the majority of registered hunters purchased either one or two licenses and assumes that they maintained their 2004 listed state of residency; were active throughout the 3-year period; and that, all things being equal, will hunt in their home state.
*Data only available for May, June, and September.
†Data only available for December.
N/A, not available.

need for some degree of habitat continuity across international borders.

Our ability to generalize movement data to all *P. vampyrus* is limited by the small number of bats collared, the bias towards male bats, which also tend to be larger, and the lack of long-term telemetry data from individuals. Annual seasonal movement trends could not be assessed. We chose larger bats to minimize the burden of the transmitter, keeping it to $< 3\%$ of body mass. Although adult female *P. vampyrus* in Peninsular, Malaysia averaged 864 g (± 198 g; J. H. Epstein, unpublished data), and may have accommodated a 22 g collar, pups are born at around 133 g (Kunz & Jones 2000) and may be carried by females for several weeks. Thus we chose not to collar females to avoid creating an additional burden. We do not know whether female bats have similar movement patterns. Female philopatry is common in many mammalian species (Greenwood 1980), although different bat species exhibit this behaviour to varying degrees (Fleming & Eby 2003), and we note that recent molecular studies of maternally inherited, mitochondrial DNA markers did not support female philopatry in *P. vampyrus* (Olival 2008). In fact, there is evidence for high levels of gene flow among *P. vampyrus* populations examined across Southeast Asia, corroborating our satellite telemetry observations of trans-boundary movement (Olival 2008).

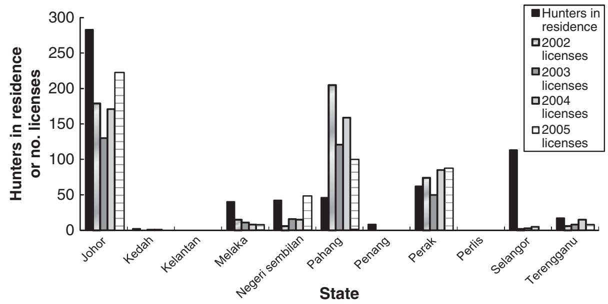

Fig. 5. State-by-state comparison of the number of registered hunters and licenses issued by year in Peninsular Malaysia, 2002–2005. Johor, Pahang, and Perak have the highest hunting activity each year.

HUNTING IMPACT AND SUSTAINABILITY

International migration of *P. vampyrus* makes it difficult to assess the impact of hunting on the entire species because our hunting data only cover Peninsular Malaysia. Even so, our

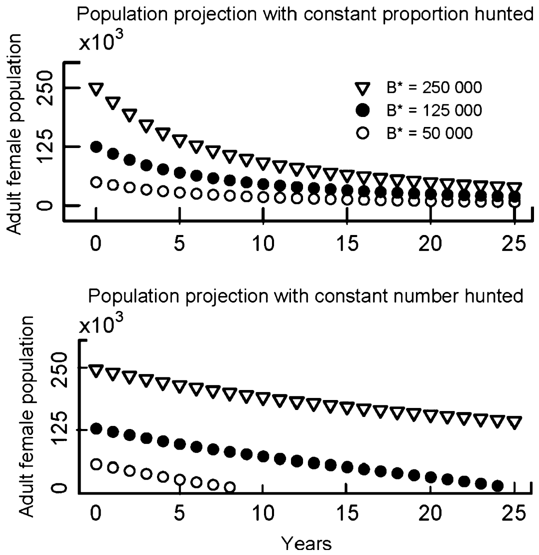

Fig. 6. Projections of *Pteropus vampyrus* population size in Peninsular Malaysia under different hunting scenarios. All model runs assume that the population begins at equilibrium (no hunting) and that a constant proportion of the bat population (Model 1, top panel) or a constant number of bats (Model 2, bottom panel) is removed by hunting each year. Three initial population levels are used (50 000, 125 000, and 250 000), each corresponding to the equilibrium population. All model runs assume an annual survival probability in the absence of hunting of $s = 0{\cdot}85$. In the top panel, the projection incorporates an additional annual mortality because of hunting of $h = 0{\cdot}10$, or 10% of the population, with a constant and equal proportion of all age classes assumed to be hunted. In the bottom panel, hunting is assumed to affect each age class in proportion to the percentage of the total population represented by the age class. We assume a constant total annual removal of H = 22 000 bats (or 11 000 female bats). Results from model runs with different parameter values are given in Tables S2 and S3 (Supporting Information).

models of the *P. vampyrus* population suggest that the level of hunting occurring in Malaysia alone is likely to be unsustainable. We found that the maximum sustainable annual yield for a population starting at an un-hunted equilibrium of 500 000 bats was *c.* 16 000 bats per year, compared with the average legal harvest in Malaysia of nearly 22 000 bats per year over the time period from 2002 to 2005. Any additional hunting of individuals from this population that occurs in Thailand or Indonesia will only hasten the population's decimation unless the baseline total population size in this region is substantially larger than the maximum population size examined here. Reports from the literature indicate widespread decline in populations for *Pteropus vampyrus* in both Peninsular and eastern Malaysia (Mickleburg *et al.* 1992; Mohd-Azlan *et al.* 2001; Struebig *et al.* 2007), and the Philippines (Mildenstein *et al.* 2005). Even with no additional hunting occurring outside Malaysia, under our best-case scenario [a life-expectancy of 20 years in the absence of hunting ($s = 0{\cdot}95$), combined with either a constant proportion or a constant number hunted annually], the non-hunted equilibrium population size would have to be nearly 900 000 bats for an annual harvest of 22 000 to be sustainable.

Our model assumptions and our estimate of hunting mortality should be considered conservative. Firstly, they assume that either a fixed proportion or a constant number of animals are taken each year, while the annual legally hunted take has been increasing over time despite decreasing population size. Secondly, the total number of hunting licenses issued by Perhilitan during the three-year period of 2003–2006 ($n = 1269$) is greater than that of the 7-year period between 1990 and 1996 ($n = 1125$), suggesting that the demand for hunting bats has more than doubled in the last 10 years (Mohd-Azlan *et al.* 2001). While this change may reflect an increase in hunter com-

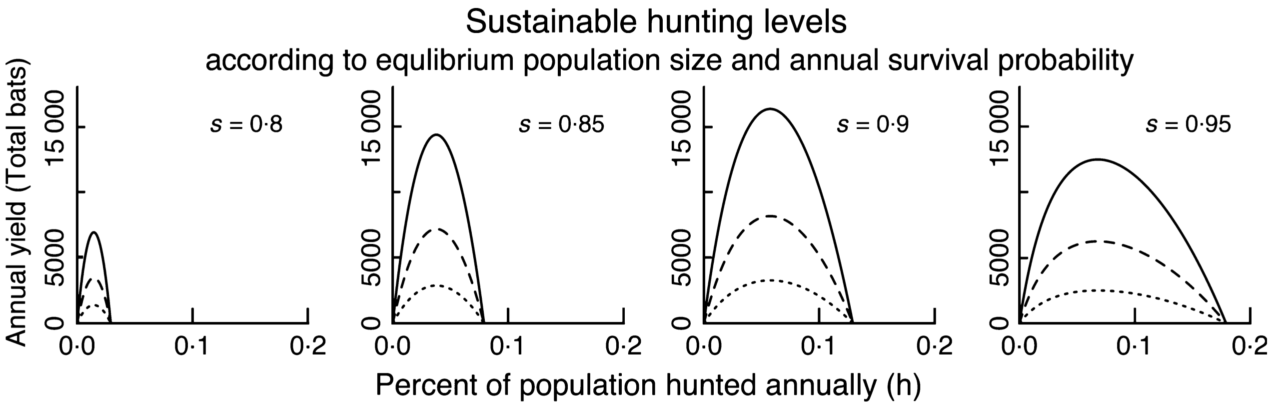

Fig. 7. Modelled response of a *Pteropus vampyrus* population to the annual removal of a constant percentage of the bat population (Model 1). The maximum allowable per cent yield and the maximum sustainable absolute yield are functions of the equilibrium size of the non-hunted population and its annual survival probability. No level of hunting is likely to be sustainable if the annual survival probability of the non-hunted population is less than *c.* 77%. In no case does the sustainable yield of bats under this model exceed 17 000. The current number of bats hunted annually in Malaysia is estimated to be 22 000, which this model suggests is likely to be unsustainable. Three scenarios are presented here corresponding to an initial adult female population size (at equilibrium, without hunting) of 50 000 bats (dotted line), 125 000 bats (dashed line), and 250 000 bats (solid line). Each panel represents a background annual mortality probability for which some level of sustainable hunting is plausible. The *y*-axis corresponds to the total annual yield of bats, and the point at which the level of hunting leads to extinction of the bat population is indicated by the point at which the yield drops to zero as the per cent of the population hunted increases.

pliance with regard to license purchases, there is no evidence to suggest that this is the case. Hunters in Peninsular Malaysia generally have vehicles and mobile phones and can move around the country quite easily which facilitates coordinated hunting activities. The hunter index supports the hypothesis that hunters are mobile and will hunt beyond their home state. It is possible that hunters may shift their activity based on reports of high local bat abundance. If the trend in license purchases corresponds to increased hunting activity in the face of decreasing *P. vampyrus* abundance, the long-term prospects for population sustainability are more dire than our projections suggest. Finally, our models do not take into account potential reductions in roosting habitat or food resources associated with deforestation throughout the bats' range (Mickleburgh *et al*. 2002), concentration of hunting effort during the reproductive season (March–August; see Fig. 4), undocumented hunting mortality because of unlicensed hunting or exceeded license limits, and unreported culling of bats as agricultural pests. Enforcement of licensed hunting is often poor (Fujita & Tuttle 1991; Mohd-Azlan *et al*. 2001; Corlett 2007), and we recorded numerous anecdotal reports from landowners and hunters who claimed to have killed more than their legal take, with some individual hunters claiming to have killed more than a thousand bats in a single year.

On the other hand, some factors could lend unexpected resilience to the *P. vampyrus* population in this region. For example, there are bioeconomic factors such as market value and cost of hunting (expensive) that may contribute to the sustainability of harvesting practices (Ling & Milner-Gulland 2006). Furthermore, if hunting pressure is substantially lower in Sumatra and Thailand than in Peninsular Malaysia, these areas could serve as source habitat. This emphasizes the importance of further characterization of *P. vampyrus* abundance in Sumatra and Thailand; movement across international borders; and the need to assess the status of hunting and habitat availability in these countries.

MANAGEMENT RECOMMENDATIONS

The conservation status of *Pteropus vampyrus* in Peninsular Malaysia was last assessed in 1999 (Mohd-Azlan *et al*. 2001) and the species is currently listed by the International Union for the Conservation of Nature (IUCN) as Near Threatened with a decreasing population trend (IUCN 2009). The Convention on the international trade in endangered species (CITES) lists *P. vampyrus* under Appendix II (all *Pteropus* spp. are included in either Appendix I or II), which describes species as vulnerable to extinction unless closely controlled (http://www.cites.org/eng/app/index.shtml). While the current lack of data on baseline population size and connectivity throughout the species' range precludes rigorous quantitative assessment of the overall viability of *P. vampyrus*, our analysis suggests that current hunting practices of *P. vampyrus* in Peninsular Malaysia are unsustainable. Currently in Peninsular Malaysia, there is no limit to the number of licenses a hunter may obtain annually. Based on our findings, a temporary ban on flying-fox hunting in Peninsular Malaysia to allow time for a regional reassessment of the status of *P. vampyrus* would appropriately prevent over-harvesting. Hunting regulations in Peninsular Malaysia are currently under review by Perhilitan. While a multi-year reduction of hunting levels may allow the population of *P. vampyrus* in Peninsular Malaysia to stabilize, incomplete hunting limits and restrictions are difficult to enforce (Mohd-Azlan *et al*. 2001). A complete hunting ban, as currently exists in the eastern Malaysian state of Sarawak, may be easier for authorities to enforce than the current regulations and may allow for *P. vampyrus* populations to recover.

Our data on the migratory nature of *P. vampyrus* in the region surrounding Peninsular Malaysia suggests that a regional focus is required for its conservation and management. Multi-national protection plans have been established for many migratory animals including birds (U.S. Dept. of State 1972; Bowman 1999; U.S. Congress 2000), marine mammals and turtles (USFWS 1972; U.S. Congress 2004), ungulates (CMS 1979) and neotropical Microchiroptera (Medellin 2003). These plans recognize that many migratory species are ecologically and economically important and require protection throughout their ranges. They also identify anthropogenic threats such as deforestation and hunting as primary risks to migratory populations. A regional approach to pteropodid conservation has previously been suggested in the literature (Mohd-Azlan *et al*. 2001) and proposed by the IUCN SSC Bat Specialist Group (Hutson, Mickelburgh, & Racey 2001). Our data, coupled with the economic and ecological importance of pteropodids, their long-range movements, and vulnerability to hunting and habitat loss across their range (Mickleburgh *et al*. 2002; Jones, Mickleburgh, & Walsh 2010), provide significant support to these proposals. A multi-national approach could be modelled on the EUROBATS treaty, adopted in 1991 (http://www.eurobats.org), which aims to protect all European bats through legislation, education, conservation, and international co-operation.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1. Model parameters

Table S2. Results from hunting model 1: removal of a constant proportion of bats

Table S3. Results from hunting model 2 (a and b): removal of a constant number

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