RAFFLES BULLETIN OF ZOOLOGY **69**: 176–187
Date of publication: 9 June 2021
DOI: 10.26107/RBZ-2021-0015
http://zoobank.org/urn:lsid:zoobank.org:pub:05E85EEC-D839-488E-94B3-83D642F63BB1

Population trends and conservation status of proboscis monkeys (*Nasalis larvatus*) in the face of habitat change in the Klias Peninsula, Sabah, Borneo, Malaysia

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Abstract. Proboscis monkey (*Nasalis larvatus*) habitats throughout its range are becoming increasingly fragmented and degraded. Discerning patterns of abundance and distribution, and elucidating factors that affect the survival of this species in altered landscapes are vital for its conservation. We assessed population trends over 10 years in the Klias Peninsula of western Sabah, Malaysian Borneo. Our findings revealed that population size and distribution remained generally stable between 2004 and 2014, and little further habitat loss occurred over this interval. However, a positive correlation in proboscis monkey abundance was found with increasing proximity to areas where more large emergent trees remained along the riverbanks. This indicates that habitat quality is an ongoing conservation concern. Furthermore, we found that only about half of the available proboscis monkey habitat in this region is fully protected. The rest is within commercial and native-titled lands that are, by law, required to be converted to agriculture. For example, we identified key proboscis monkey habitat within and around the Padas Damit Class IV Amenity Forest Reserve, an area where we also found the highest densities of proboscis monkeys in the region. However, significant areas in close proximity or contiguous with this forest reserve have subsequently been converted to oil palm. Such development not only causes outright habitat loss but also risks disrupting connectivity of proboscis monkey habitat, especially along rivers. This in turn poses a threat not only to long-term viability of the local proboscis monkey population, but also to another vital aspect of the economy of the Klias region that depends on the draw of proboscis monkey-viewing for wildlife-based tourism. We suggest that mechanisms to safeguard the contiguity of remaining proboscis monkey habitat within this area should be implemented at the landscape level to ensure persistence of the local population.

Key words. abundance and distribution, Klias Peninsula, proboscis monkey, landscape conservation, connectivity, fragmentation

INTRODUCTION

Nearly half of all non-human primates are threatened with extinction from habitat loss, degradation, and fragmentation due to anthropogenic factors such as logging and expansion of industrial agriculture (Estrada et al., 2017). A fundamental wildlife management issue is the lack of basic information, such as abundance and distribution, necessary for developing effective management plans for long-term conservation. Because primates are long-lived mammals with slow life cycles, they generally respond very slowly to dramatic environmental changes and human interference (Chapman et al., 2006). Therefore, basic long-term monitoring data, such as population size and distribution range, are indispensable for understanding population trends, particularly in relation to changes in habitat quality and anthropogenic impacts (Chapman et al., 2017).

Agriculture, especially of oil palm (*Elaeis guineensis*), has replaced large areas of forest in Southeast Asia, a region with several global biodiversity hotspots (Myers et al., 2000; Fitzherbert et al., 2008). Borneo, in particular, has been identified as a centre of endemism, yet its forests remain highly threatened by small- and large-scale conversion of forest to oil palm (Sodhi et al., 2004; Woodruff, 2010; Abram et al., 2014). As a result, Bornean primates living in these regions have suffered significantly from forest losses (Wich et al., 2012; Ancrenaz et al., 2014; Abram et al., 2015; Bernard et al., 2016), as well as hunting, another major threat that has caused the decline of many primate populations in Borneo (Bennett et al., 2000; Corlett, 2007; Harrison, 2011; Davis et al., 2013).

Accepted by: Chong Kwek Yan

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ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

The proboscis monkey (*Nasalis larvatus*), a Bornean endemic species, has been red-listed by the IUCN as an Endangered species since 2000 (Boonratana et al., 2020). Proboscis monkeys are large, sexually dimorphic, diurnal arboreal colobines (Koda et al., 2018). Their typical social unit is a unimale, multi-female group, consisting of an adult male, several adult females, and immatures, although there are also all-male groups that consist mainly of young males (Bennett & Sebastian, 1988; Yeager, 1990). Proboscis monkeys are closely associated with waterways and inhabit mainly riverine forests, mangrove, and lowland peat swamps (Sha et al., 2008). However, such habitats are becoming increasingly threatened by the conversion to industrial agricultural plantations, mainly oil palm, which requires these same lowland floodplain areas (Meijaard & Nijman, 2000a; Gaveau et al., 2014). As a result, agricultural expansion and forest fragmentation have been shown to exert considerable negative impacts on proboscis monkey population size and distribution island-wide (Meijaard & Nijman, 2000b; Matsuda et al., 2020; Toulec et al., 2020). Other identified causes of proboscis monkey habitat loss and fragmentation are logging, fire, and expanding pockets of human habitation (Sha et al., 2008).

A state-wide proboscis monkey survey in the East Malaysian state of Sabah, Borneo, was conducted in 2005 by boat-based methods along major rivers and tributaries (Sha et al., 2008). The 2005 survey revealed that the Klias Peninsula region located in western Sabah had an estimated total of 818 individual proboscis monkeys in 75 groups. A year earlier, in 2004, a similar but more localised survey covering the Klias Peninsula region was conducted by Bernard & Zulhazman (2006). Their survey recorded an estimated overall total of 569 individuals in 65 groups. Both surveys concluded that in 2004 and 2005 the Klias population was one of the remaining proboscis monkey strongholds in Sabah and likely contained the only viable population of this primate species in the entire west coast region of the state (Bernard & Zulhazman, 2006; Sha et al., 2008). Due to the reliable presence of proboscis monkeys, the Klias Peninsula is also regarded as an important region for wildlife-based tourism in Sabah. This has resulted in a major proliferation of large- and small-scale tourist establishments, particularly over the past 15 years, to cater to the increasing visitor volume (Sha et al., 2011).

In this latest census survey completed in 2014 and reported here, we determined abundance and distribution patterns of the local proboscis monkey population in the Klias Peninsula region and compared this with earlier results from Bernard & Zulhazman (2006) and Sha et al. (2008), completed approximately 10 years earlier (in 2004/2005). We used the same methods and followed generally the same routes as the previous studies. Our aim was to measure any change in proboscis monkey population trends in relation to habitat degradation and agricultural conversion in the area between 2004 and 2014. We also derived land-use and land-cover statistics and used information on allocated land titles and forest reserves to calculate the extent of potential proboscis monkey habitat that is under threat and/or earmarked for conversion, as a window into the possible future for the population in the Klias Peninsula of Sabah. Additionally, we elucidate some factors affecting proboscis monkey abundance by modelling variations in relation to aspects of habitat quality (i.e., vegetation) and other anthropogenic factors, including oil palm plantations and human settlement development. We predicted that higher habitat quality will contribute positively to proboscis monkey abundance whereas anthropogenic activities would have a negative effect. We also expected an overall decline in proboscis monkey abundance between 2004 and 2014 due to land-use changes during those periods (Kamlun et al., 2016).

METHODS

Study area. The study area was located mainly along the Padas River, Padas-Damit River, Klias River, and Bukau River in the Klias Peninsula, western Sabah, East Malaysia. Overall, the Klias Peninsula covers an area of 130,000 ha, and is characterised by generally flat land (0–50 m a.s.l.) (Bernard & Zulhazman, 2006). The predominant vegetation throughout the Klias Peninsula consists of a complex mixture of mangrove, nipah palm forest, freshwater swamp forest, and peat swamp forest in various states of degradation, interspersed with open areas and extensive wet grasslands (Bernard et al., 2019a). Prior to this study, a large proportion of the natural vegetation had already been heavily disturbed and fragmented, with large areas cleared to make way for human settlements, subsistence agriculture (mainly for wet paddy), rubber trees and, more recently and extensively, small- and medium-sized oil palm estates (Kamlun et al., 2016). During the study period the mean minimum and maximum temperatures were 22 and 35°C, respectively. Annual precipitation in the study region was between 3,000 and 3,500 mm (Sabah Meteorological Department, 2015).

We selected seven sampling sites (Fig. 1) within and/or in the vicinity of protected areas, scattered around the Klias Peninsula region as follows: (1) Padang Teratak Bird Sanctuary, (2) Padas Damit Forest Reserve, (3) Menumbok Forest Reserve, (4) Binsulok Forest Reserve, (5) Klias Forest Reserve, (6) Kg. Hindian Forest Reserve, and (7) Nabahan Forest Reserve. Previous studies conducted in 2004/2005 had confirmed the presence of proboscis monkeys in all of the above sampling sites (Bernard & Zulhazman, 2006; Sha et al., 2008).

Boat-based river survey of proboscis monkeys. Proboscis monkey habitats throughout their range are generally always wet, therefore the most efficient and cost-effective way to survey monkeys living in flooded forest habitat is by boat (Matsuda et al., 2016). Furthermore, this monkey species customarily returns almost every evening to sleep in trees located along riverbanks. This daily ranging pattern, common throughout their range on Borneo Island, is also observed in the Klias Peninsula region (Bennett & Sebastian, 1988; Yeager, 1989, 1995; Sha et al., 2008; Matsuda et al., 2010). Therefore, we employed the classic boat-based method to conduct surveys during early mornings and/or late afternoons,

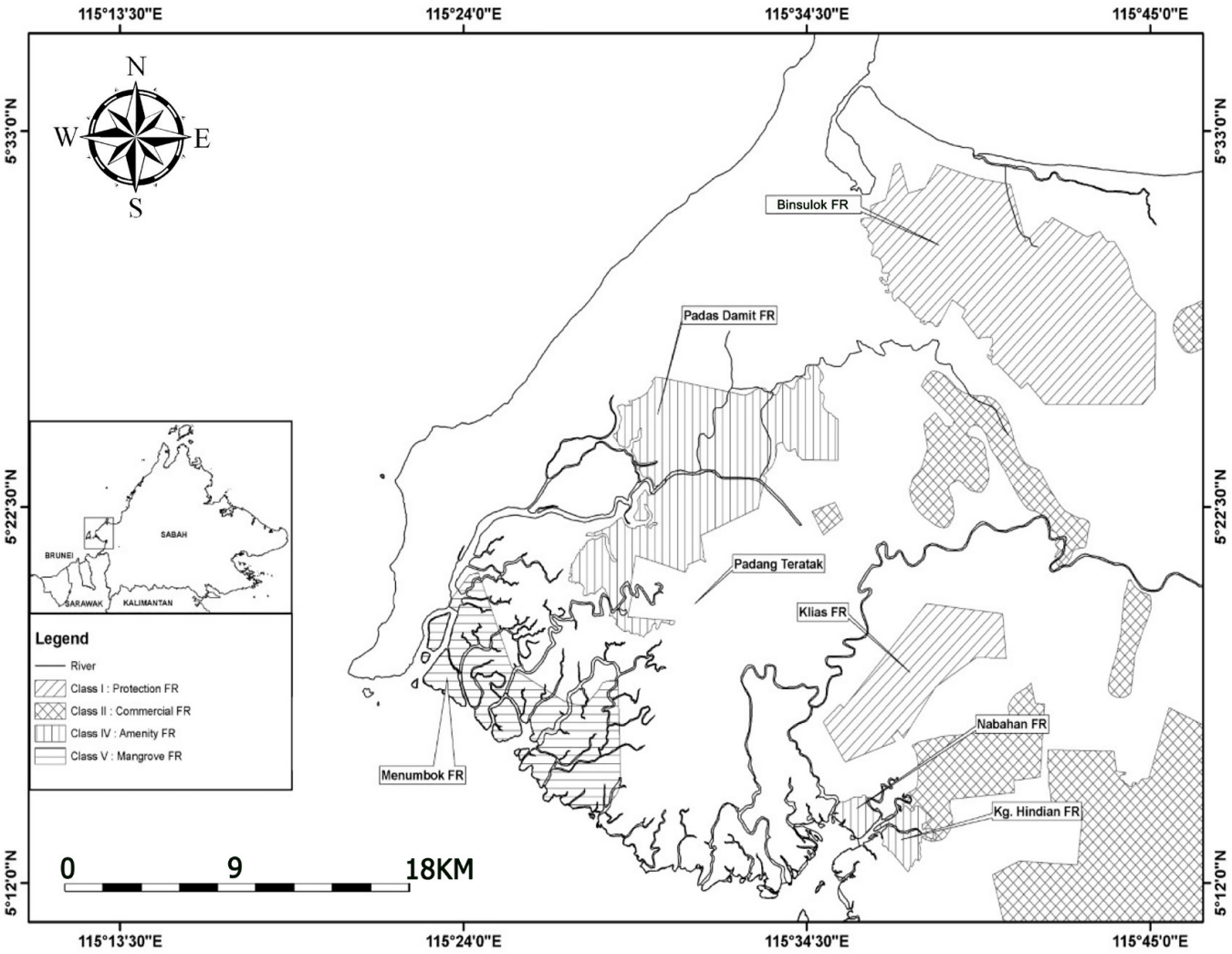

Fig. 1. Map showing the Klias Peninsula region in western Sabah, in the northern part of Borneo (inset), Malaysia, and the research sampling sites in riverine, mangrove, and mixed mangrove-riverine forests along rivers in Padang Teratak Bird Sanctuary, Padas Damit Forest Reserve, Menumbok Forest Reserve, Binsulok Forest Reserve, Klias Forest Reserve, Kg. Hindian Forest Reserve, and Nabahan Forest Reserve, where the river surveys of the sleeping sites of proboscis monkeys were conducted.

i.e., shortly before the monkeys leave their sleeping trees in the morning or when they have just entered their sleeping sites in the late afternoon. Specifically, we performed the surveys from 0530 to 0930 hours and/or from 1600 to 1830 hours from January to March 2014, to document the abundance and distribution of proboscis monkeys in the above-mentioned seven sites. We surveyed all main rivers and their tributaries only once without repeat surveys. We covered rivers and tributaries that were in close proximity to each other in one survey session or on consecutive days to minimise the probability of double-counting. At each site we surveyed a distance ranging from 6.5 to 21.7 km, with a total surveyed distance of 106 km (Table 1). Whenever we spotted proboscis monkeys in the trees, we recorded the group location using a global positioning system (GPS) receiver. We also recorded the total number observed in each group and the group type, i.e., either a unimale, multi-female group, or an all-male group. In addition, we recorded the habitat type where the group occurred following the general habitat classification by Bernard et al. (2019a), i.e., (1) mangrove, (2) riverine, or (3) mixed mangrove-riverine forests. We identified the total distance surveyed of each habitat type by traversing the river by boat and determining the length covered by each of the three habitat classes along the riverbanks using a GPS receiver. We assessed the relative habitat preferences of proboscis monkeys observed in each habitat type by dividing the total number of individuals detected over the length of the riverbanks covered by each of the three different habitat types.

Vegetation survey. To assess vegetation characteristics at each sampling site, we set up four to six circular plots (40 m in diameter per plot) at each site for an overall total of 34 vegetation plots. The objective was to focus our vegetation assessments on the sites where proboscis monkeys were frequently encountered, such as their sleeping sites located in close proximity (< 50 m) to riverbanks. However, because of the swampy habitats and dense undergrowth associated with wetland forests, and habitat fragmentation sometimes leaving only small intact vegetation areas along the rivers, options for vegetation plots in some sites were limited to nearer rather than more inland from the river banks. We labelled all trees ≥ 10 cm gbh (girth at breast height) located within the plots and identified them with the support of a botanist from the

Table 1. Summary of the river surveys for proboscis monkey populations in each site.

Study site	Area size (km^2)	Distance of river surveyed (km)	No. of individuals detected	No. of groups detected	Individual density (ind./km^2)	Group density (grp./km^2)
Padang Teratak	27.50	10.0	46	4	1.7	0.15
Padas Damit	90.30	21.7	200	21	2.2	0.23
Menumbok	20.00	20.5	120	10	6.0	0.50
Binsulok	121.10	11.6	56	8	0.5	0.07
Klias	36.20	17.0	91	13	2.5	0.36
Kg. Hindian	5.80	6.5	94	8	16.2	1.38
Nabahan	3.56	18.7	72	11	20.2	3.09
Total/all sites combined	304.50	106.0	679	75	2.2	0.25

Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah. We measured the gbh of all labelled trees. Based on the data recorded from the vegetation plots, we calculated three vegetation variables, i.e., (a) tree basal area: sum of the area of all tree stems (m^2) in a plot; (b) tree species richness: number of the recorded tree species in a plot; and (c) maximum tree diameter: diameter (cm) of the tree with the largest gbh size in a plot.

Anthropogenic activities. We measured two variables associated with anthropogenic activities as follows: (A) the nearest distance from agriculture, specified by measuring the distances (km) from the centre of each survey site to the edges of three nearest agricultural sites; and (B) the nearest distance from human settlement areas, as measured by determining the distances (km) from the centre of each sampling site to the edges of three nearest human settlements. We estimated all geographic distances using the distance tool in Google Earth Pro. Version 9.2.63.0.

Abundance data analysis by area rather than linear measure. We calculated relative abundance at each of the sampling sites by dividing the sum of the proboscis monkey count with the size of the sampling sites. We chose to measure proboscis monkey abundance proportional to the size of the study sites rather than to the length of the rivers surveyed. Indeed, distance surveyed along rivers is also relevant. However, because the rivers surveyed in this study were quite meandering (winding) and rarely straight, the study sites covered in our surveys were better represented by an area measure than a linear one.

Data analysis of the effects of vegetation and anthropogenic factors. We examined the effects of the vegetative variables, (a) tree basal area, and (b) tree species richness, on proboscis monkey population density (km^2) in each survey site, using a simple linear regression analysis; note that as variables (a) tree basal area and (c) maximum tree diameter were highly correlated (Spearman's rank correlation coefficient: rho = 0.81 and p-value < .0001), we did not test the effect of the variable (c). The proboscis monkey counts in each sampling site per size of the sampling site were treated as a dependent variable with a Box-Cox transformation prior to analysis to satisfy the model assumptions of normally distributed residuals (Beaty et al., 1985). We used the Bonferroni correction to correct for multiple comparisons of those linear regression analyses (P = 0.05/N: N is the number of comparisons made, i.e., 0.025). A simple linear regression analysis was also performed to find out whether proboscis monkey population density (km^2) in each survey site was affected by the two sets of anthropogenic variables, (A) the nearest distance from agriculture, and (B) the nearest distance from human settlement areas. We used the Bonferroni correction to correct for multiple comparisons of those linear regression analyses (P = 0.05/N: N is the number of comparisons made, i.e., 0.025). All analyses were performed in R ver. 3.1.0 (R Core Development Team, 2019).

Temporal land use and land cover in proboscis monkey range. To understand the extent of proboscis monkey habitat in the Klias Peninsula and calculate habitat lost between 2004 and 2014, we performed basic spatial analyses for the 2004/2005 and 2014/2015 timeframes. We first identified the rivers surveyed for proboscis monkeys, then defined the proboscis monkey's potential range (using the buffer tool in ArcGIS 10.8.1) for the surveyed regions by setting a 1-km boundary from the riverbank. Matsuda et al. (2010) suggested that 800 m is typically the distance that proboscis monkeys would travel from riverbanks, whereas Stark et al. (2017b), based on a study that used collared GPS data, showed that the maximum distance travelled by proboscis monkeys from riverbanks was up to 2 km, although this was not typical. Based on this prior information, we decided to use a 1-km distance. Within the 1-km buffer areas, we then digitised various land-use and land-cover types. For 2014/2015, we used high-resolution (1.5 m) SPOT 5 imagery, which allows for easier identification of land-use and land-cover types, and enabled us to undertake detailed, fine-scale mapping. For 2004/2005, no SPOT imagery was available to us, so we used a combination of Landsat (30 m) and Google Earth

images. Due to the high resolution of the SPOT imagery, we undertook the mapping for the 2014/2015 time period first, as these images allowed us to better understand the various land-use and land-cover classes present within the study region, and enabled us to map, with precision, these various classes. After completing the 2014/2015 classification, we turned to the 2004/2005 mapping. To do this, we used the 2014/2015 layer as our starting point, then used Landsat imagery and good imagery from Google Earth for 2004/2005 to help identify where land-use and/or land-cover changes had occurred within the 10-year period. Where there were changes, we used both Landsat and Google Earth imagery to map the extent of these changes and to identify the land-use/land-cover category for that area in 2004/2005.

The land-use/land-cover categories digitised within the potential proboscis monkey range included: (1) intact forested areas that were identified as mangroves; (2) intact forested areas that were likely to be riverine forests and freshwater swamp forest types; (3) degraded forested and swamp areas, with sparse tree composition (degraded forests and natural swamps were pooled together as we were unable to distinguish one from the other through satellite imagery); (4) areas of oil palm that were split into three sub-classes that included estates, smallholdings, and areas that have potentially failed oil palm due to flooding and unsuitable lands (see Abram et al., 2014); (5) mixed mosaic areas that included human settlements and various smallholdings with potential fruit trees and other community land use types; (6) wet paddy areas; (7) agroforestry areas; and (8) aquaculture.

Identifying protected habitat and habitat under threat of conversion. To identify the extent of protected potential proboscis monkey habitat in the Klias Peninsula, we used data from the Sabah Forestry Department for Sabah's various Protected Area designations (i.e., various Protection Forest Reserves, Parks, and Wildlife Sanctuaries) as well as various commercial Production Forest Reserves.

To also understand the extent of potential proboscis monkey habitat under threat outside of Protected Areas and Production Forest Reserves, we used land title data to estimate the overlap between unprotected forests and allocated land titles granted (or 'alienated') by the government (largely for oil palm). These land title data were obtained from the Sabah government's Land and Survey Department's online platform (www.jtuwma.net) accessed on 2 February 2017. The data were in shapefile polygon format and included a number of land title types. Land title types included: (1) Field Register (FR), which is a temporary status before Native Title (NT) is granted; (2) Native Title (NT), which is meant for indigenous peoples for perpetuity (999 years), restricted to less than 40 ha in size, and typically granted for oil palm, rubber, and other agricultural smallholdings; (3) Provisional Lease (PL), which is given prior to the Country Lease (CL) title; and (4) Country Lease title, which is open to all citizens and non-citizens of Malaysia for a 99-year period and usually given for the purpose of agriculture (largely oil palm) (Sabah Land Ordinance, 1976). Additionally, in the land title dataset, there were demarcated land titles with no codes, which we assumed to be land under application and refer to as 'unknown titles'. Lastly, we also identified potential 'State Land' (i.e., land that has not been alienated to any type of land title and that is not in any Protected Area or Production Forest Reserve) by extracting land that was outside of the land title, Protected Areas, and Production Forest Reserve datasets. State Lands are lands that are available for land applications by individuals or companies under the Sabah Land Ordinance (1976), or are available for government purposes, e.g., for protection purposes.

RESULTS

Population abundance and distribution pattern. We conducted a total of 42 boat-based proboscis monkey surveys over 35 field days in the seven study sites. Overall, we detected a total of 679 individuals in 75 groups across all the study sites (44 unimale, multi-female groups; 16 all-male groups—including solitary males; and 15 groups for which the composition could not be determined). The highest abundance, with 200 individuals and 21 groups, was recorded in the Padas Damit Forest Reserve situated in the central part of the Klias Peninsula (Table 1). Based on the three general habitat classifications used in this study (following Bernard et al., 2019a), proboscis monkey groups were detected in only two habitat types, namely riverine and mangrove forests. The distances surveyed along riverbanks that were covered in riverine, mangrove, and mixed mangrove-riverine forests were approximately 35, 65, and 5 km respectively. Although more individuals were detected in the mangroves (412) than in riverine forests (267), the corrected relative habitat preference values, i.e., weighted by the distance surveyed along all three habitat types, revealed that more monkeys were found in the riverine forests (7.6 individuals/km) than in mangroves (6.3 individuals/km).

Effects of vegetation variables and anthropogenic activities on population abundance. Measurements of the vegetation variables varied across the sites and within each site (Fig. 2). The sites which had different forest types (i.e., riverine forests, mangrove forests, and mixed mangrove-riverine forests) showed a large variation in the vegetation variables recorded, such as at Kg. Hindian. The population density of proboscis monkeys was significantly and positively associated with the total basal area of trees (R^2: 0.12 and p-value: 0.024); the model for tree species richness was not statistically significant (R^2: −0.023 and p-value: 0.625). These results generally indicate that proboscis monkeys were concentrated in sites with larger/emergent trees, hence suggesting that these areas are especially important as nighttime sleeping sites. Analysis of the anthropogenic variables showed that distances from both agricultural sites (with a positive effect: R^2: 0.06 and p-value: 0.59) and human settlement areas (with a negative effect: R^2: −0.05 and p-value: 0.70) were not significantly associated with the population density of proboscis monkeys.

Forest loss. From 2004/2005 to 2014/2015, a total of 1,152 ha of intact forest (mostly intact riverine forest, at 1,145 ha)

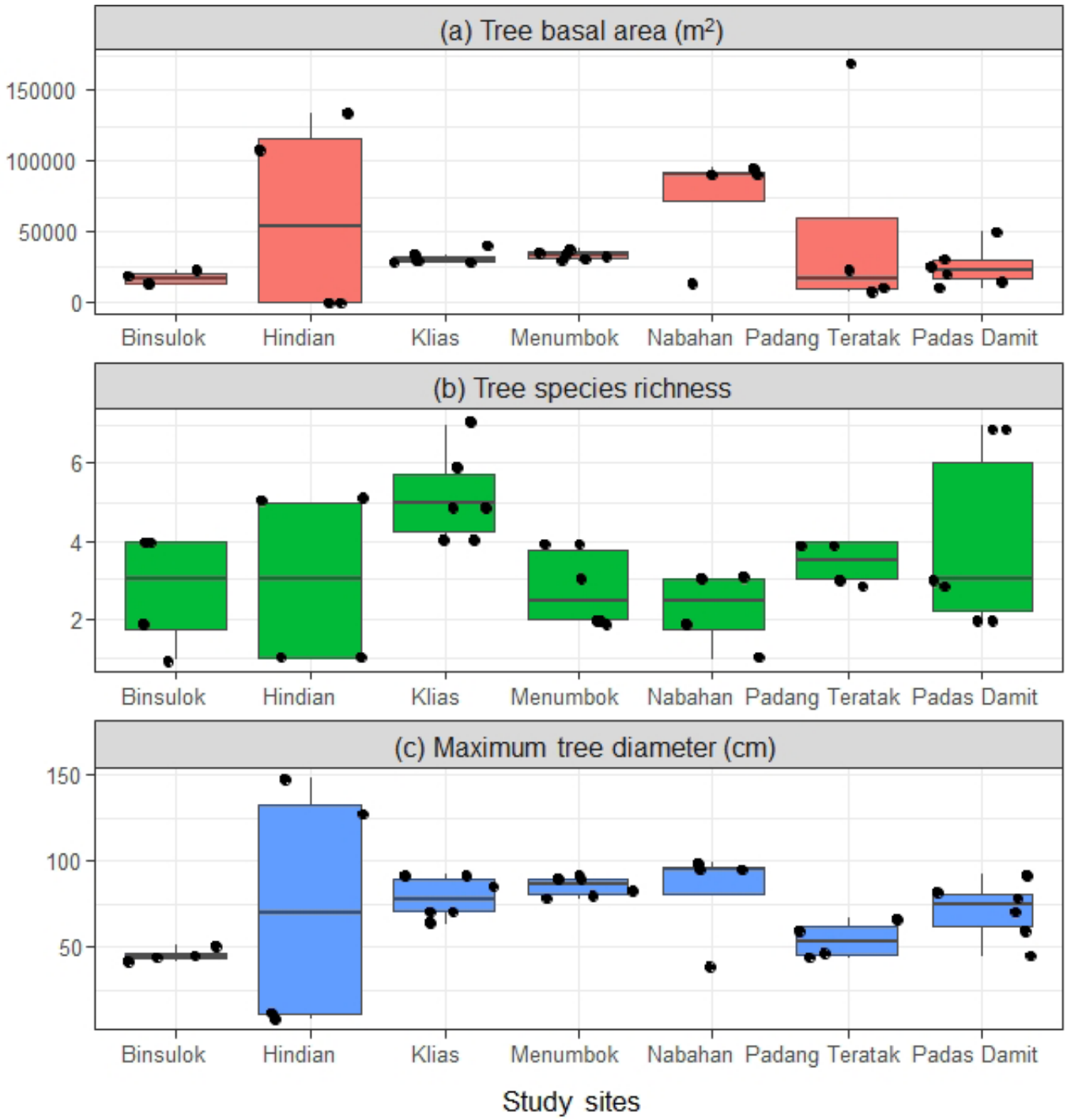

Fig. 2. Boxplots illustrating the variation in vegetation variables, with each point representing the values for vegetation plot in each site.

and 1,196 ha of degraded forest and swamp areas were lost largely to oil palm, which saw a gain of 2,321 ha within the potential proboscis monkey range (Table 2). Of this newly planted oil palm, 94% (or 2,186 ha) was identified as potentially economically unprofitable due to inundation and/or swampy conditions (Table 2).

In 2014/2015, intact mangrove forest encompassed around 49% of the proboscis monkey range, whereas other intact forest types (likely to be riverine forest) made up an additional 11% of suitable habitat within the surveyed area, and degraded forest and swamp areas that had sparse tree composition added a further 18% of the proboscis monkey range (Table 2). This suggests that 78% of the potential proboscis monkey range had suitable (60%) or marginally suitable (18%) habitat for proboscis monkeys. Oil palm occupied 14% within the potential proboscis monkey range, mixed community land uses a further 7%, and aquaculture 1% (Table 2); these are land cover types that proboscis monkeys typically do not utilise.

Not all of the potential proboscis monkey habitat indicated above has protected status. Of the intact riverine and mangrove forest habitat, only 52% is protected (i.e., 20% of riverine forest and 59% of mangrove forest are protected), and only 6% of degraded forest/swamp areas (a marginal

Table 2. Land-use and land-cover types and extents within the 1-km buffer from surveyed rivers in the years 2004/2005 and 2014/2015.

Land-use/land-cover type within potential proboscis monkey range	Extent in 2004/2005 in ha (%)	Extent in 2014/2015 in ha (%)
Forest (riverine)	7,264 (13%)	6,119 (11%)
Forest (mangrove)	27,036 (49%)	27,029 (49%)
Degraded forest and swamp areas	10,830 (20%)	9,634 (18%)
Mixed mosaic community areas	3,785 (7%)	3,812 (7%)
Oil palm (estate)	1,450 (3%)	1,499 (3%)
Oil palm (smallholdings)	1,634 (3%)	1,720 (3%)
Oil palm (underproductive)	2,244 (4%)	4,430 (8%)
Paddy	221 (< 1%)	221 (< 1%)
Agroforestry estate	16 (< 1%)	16 (< 1%)
Aquaculture	349 (1%)	349 (1%)
Total extent	54,829	54,829

Table 3. Extents of forest (generic forest category and mangrove) and swamp/degraded area in hectares in 2014/2015 (with %) within Protected Areas, Production Forest Reserves, various alienated land titles, unknown title type, and areas with no cadastral data that may be State Land.

Land allocation	Extent of riverine forested areas in ha in 2014/2015 (%)	Extent of mangrove forested areas in ha in 2014/2015 (%)	Extent of swamp/degraded forested areas in ha in 2014/2015 (%)
Protected Areas	1,239 (20%)	15,934 (59%)	573 (6%)
Production Forest Reserves	1,182 (19%)	3,446 (13%)	4,117 (43%)
Country Lease titles	454 (7%)	1,285 (5%)	379 (4%)
Provisional Lease titles	144 (2%)	86 (< 1%)	24 (< 1%)
Native Titles	1,622 (27%)	1,467 (5%)	1,909 (20%)
Field Register titles	58 (1%)	37 (< 1%)	171 (2%)
Unknown title type	353 (6%)	468 (2%)	845 (9%)
Potentially State Land	1,067 (17%)	4,306 (16%)	1,616 (17%)
Total extent	6,119	27,029	9,634

habitat for proboscis monkey) are protected (Table 3; Fig. 3). This means that 80% of riverine forest, 41% of mangrove forest, and 94% of degraded forest/swamp areas may be at risk of conversion.

Furthermore, 14% of forest (19% of riverine forest and 13% of mangrove forest) was found in Production Forest Reserves. Of this, 1,692 ha of forest was in Class V Mangrove Forest Reserves (all of which was mangrove forest), and 2,936 ha of forest was in Class IV Amenity Forest Reserves (i.e., 1,182 ha of riverine forest and 1,754 ha of mangrove forest), which allow some degree of use (Table 3).

Also of great concern is the extent of relatively intact and degraded forest and swamp areas that are within land titles that have been granted (or 'alienated') by the Land and Survey Department for development. We found that around 27% of forest habitat is on alienated land titles; 15% (5,062 ha) is on Country Lease and Provisional Lease titles, and 9% (3,187 ha) is on Native Titles and Field Register titles. If we divide this into riverine forests and mangrove forest habitats, 43% (2,631 ha) of riverine forest habitat is located within alienated land titles, of which most is under Native Titles (Table 3); and around 13% (3,343 ha) of mangrove habitat is located within alienated land titles, largely under Native Titles and Country Lease titles (Table 3). Around 35% (3,328 ha) of degraded forest and swamp areas were identified in alienated land titles, with most of these (20%) found within Native Titles (Table 3). Importantly, for riverine forest, mangrove forest, and degraded forest/swamp

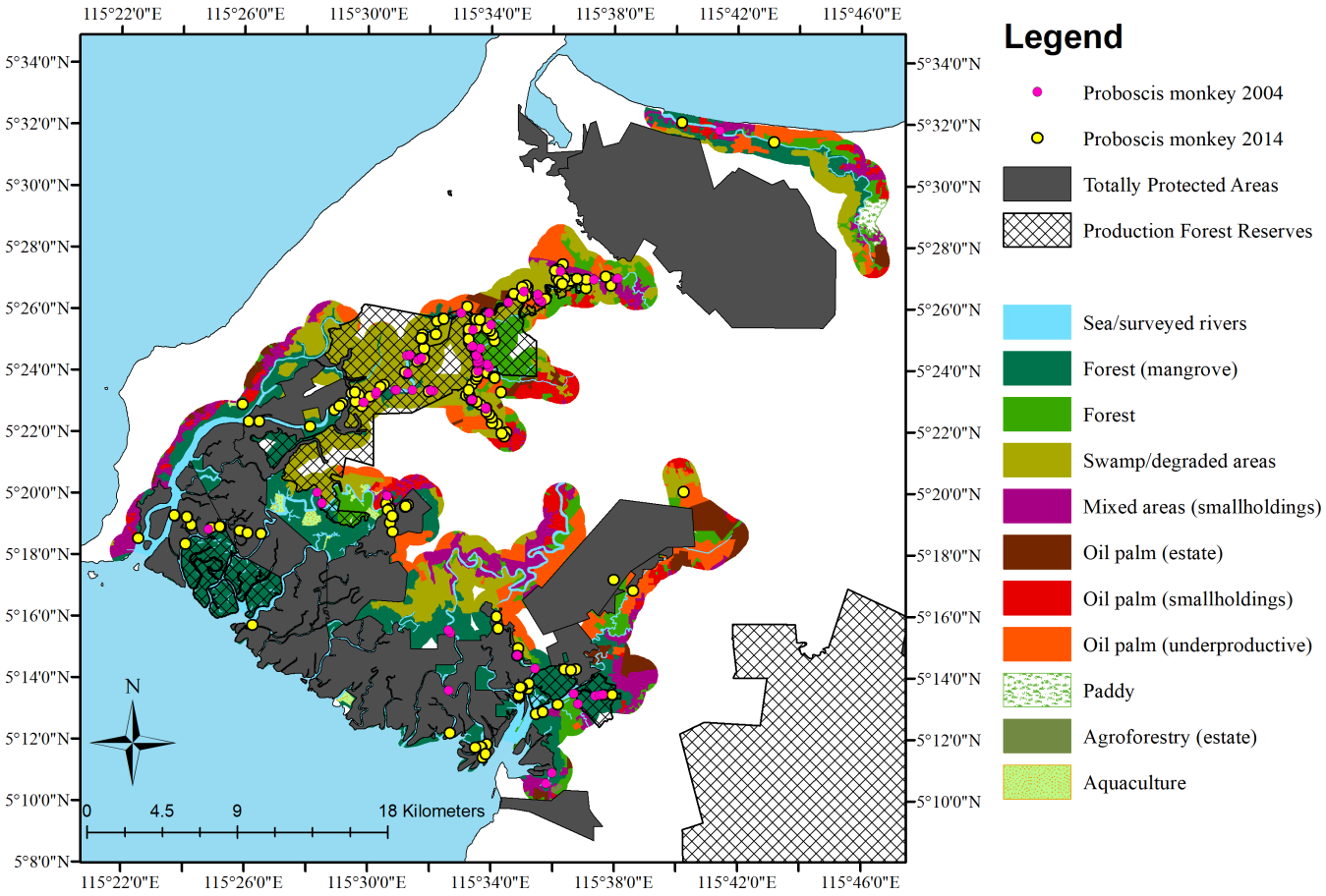

Fig. 3. Land use and land cover data for 2014/2015 within the 1-km buffer distance from surveyed rivers, overlaid with proboscis monkey sightings from the 2004/2005 and 2014 surveys, Protected Areas, and Production Forest Reserve boundaries.

habitat, around 16 to 17% of each was identified as being potentially located on State Land (1,067 ha, 4,306 ha, and 1,616 ha, respectively) (Table 3), and therefore at risk of being alienated if people or companies apply for these lands under the Sabah Land Ordinance (1976).

DISCUSSION

Population abundance, distribution pattern, and effects of vegetation variables. We found proboscis monkeys along river systems in all seven sites surveyed in the Klias Peninsula. Our results also revealed that most proboscis monkeys were found in the central part of the Klias Peninsula within and around the Padas Damit Class IV Amenity Forest Reserve, indicating that this area is a population stronghold for the species in the region. This distribution pattern was also consistent with previous regional findings using comparable survey techniques in 2004/2005 (Bernard & Zulhazman, 2006; Sha et al., 2008). The population size found in this study of 679 individuals in 75 groups compared favourably with previous estimates in 2004/2005, of 569 individuals in 65 groups (Bernard & Zulhazman, 2006) to 818 individuals in 75 groups (Sha et al., 2008), respectively. Taking into account differences in survey frequency, local conditions, monkey social dynamics, and expected variations in observational error across the three surveys by different teams, it is fair to conclude that the abundance of proboscis monkeys in the Klias Peninsula remained stable in the interval between 2004 and 2014. That is, not only do proboscis monkeys appear to still be found in the same areas in 2014 as in previous surveys conducted 10 years ago; the population size has also remained relatively stable between these time periods. This optimistic finding is very likely due to the fact that there was also relatively little proboscis monkey habitat loss during these 10 years. Specifically, we found that between 2004 and 2014, there was only a 2% reduction in riverine forest, no loss of mangrove forests, and a 2% loss of areas regarded as degraded swamp forest (Table 2).

Our study also revealed that proboscis monkeys were not evenly distributed across different habitat types. More individuals were found in the riverine forests (7.5 individuals/km) than in mangroves (6.3 individuals/km) or mixed mangrove-riverine forests (0 individuals/km). It must also be noted that the finding of 0 individuals in mixed mangrove-riverine forests may be an artefact as only 5 km of this habitat type was surveyed. However, the apparent preference for riverine forest to mangrove or mixed mangrove-riverine forests is consistent with previous studies elsewhere (e.g., Salter et al., 1985; Sha et al., 2008), as well as in Sukau, within the Lower Kinabatangan region of eastern Sabah (Matsuda et al., 2020). This is likely due to higher food availability and greater plant diversity in riverine forest habitat compared to mangrove and mixed mangrove-riverine forest (Bernard et al., 2019a). Additionally, seasonal variation in the availability

of food also prescribes habitat use in this species, and access to resources varies with fluctuating levels of resource competition with other sympatric primate species (Matsuda et al., 2019). Nevertheless, our findings indicate that both riverine and mangrove forests are essential habitats for the proboscis monkey in the Klias Peninsula. Future research to determine patterns of seasonal resource availability and nutritional quality in the three different habitat types in the Klias Peninsula is needed to better understand the role that feeding ecology plays in the distribution and ranging patterns of these monkeys in the face of anthropogenic land-use change.

In terms of vegetation characteristics, we found that the availability of suitable sleeping trees (i.e., large/emergent trees) along riverbanks could be a key limiting factor for the abundance and/or distribution patterns of proboscis monkeys at our study sites. We found the total basal area (which correlates generally to larger overall size) of trees in the vegetation plots, with a maximum tree diameter of 148 cm, to be positively associated with higher proboscis monkey abundance. In addition to providing sleeping sites for the proboscis monkeys, larger trees, usually with more main branches (i.e., horizontal volume), may better facilitate group cohesion, sociality, and communication (Matsuda et al., 2008; Bernard et al., 2011; Feilen & Marshall, 2014, 2017; Thiry et al., 2016). Furthermore, larger trees provide better protection from terrestrial predators such as clouded leopards, as it is riskier for these large-bodied predators to hunt monkeys on thinner branches high above the ground (Matsuda et al., 2008; Bernard et al., 2011).

Effects of anthropogenic activities on population abundance. In terms of anthropogenic activities, our results failed to suggest a relationship between proboscis monkey population density and distance from agricultural areas (oil palm plantations) or human settlements. It is possible that distance alone is an insufficient metric to measure anthropogenic effect on local proboscis monkey population density, although the small sample size in our study is also a possible factor in this result (n = 7 sites). Lower abundance in and around oil palm-cultivated areas is common, not only in proboscis monkeys but also for other Bornean primates, due to the lack of suitable food resources and disturbance from human activities within the stands of this monoculture exotic crop (Bernard et al., 2016). Although macaques and orangutans both feed on oil palm fruits to some extent, and male orangutans in particular also travel considerable distances to cross plantations between forest fragments, proboscis monkeys are much less likely to forage or travel very far within oil palm plantations (Sha et al., 2008; Ancrenaz et al., 2014; Bernard et al., 2016; Stark et al., 2017a; Bernard et al., 2019b; Ancrenaz et al., 2021).

In the Klias Peninsula, human settlement areas at some sites extend to the forests along the riverbanks where we frequently detected proboscis monkey groups, although the majority of settlement areas are still far from the usual proboscis monkey range (> 2 km). Indeed, larger groups of proboscis monkeys have also been detected in the lower Kinabatangan, Sabah, even very close to villages (Matsuda et al., 2020), especially if taller, overhanging trees are still found along the river banks (Matsuda et al., 2008) and individual residents nearby are tolerant of their presence (Felicity Oram, personal observation). Therefore, proboscis monkeys may be able to cope with the presence of human settlements to varying extents depending on local circumstances. Nonetheless, in the near future, there is a real possibility that increasing human activities associated with settlement areas will lead to progressive increases in disturbance, through further habitat loss to agriculture for subsistence farming, as well as an increased potential of forest fires associated with slash-and-burn activities in this region (Bernard et al., 2019b). The threat of forest fires to peat swamp forests in the Klias Peninsula is significant and particularly evident during extended droughts associated with El Niño events (Phua et al., 2007). Illegal hunting activities may also be more likely to take place adjacent to human settlement areas (Sha et al., 2008; Bernard et al., 2019b).

Forest loss. Although we found little overall habitat loss between surveys, only 20% of remaining riverine forest habitat and 59% of mangrove forest habitat (52% of these forests if aggregated) are currently within designated Protected Areas (Table 3). Of great concern is the 28% (9,080 ha) of riverine and mangrove habitats identified as 'alienated' lands (Table 3). This land designation requires, by law, time-bound conversion to specified land-use types (e.g., oil palm) as decreed under the Sabah Land Ordinance (1976). Provisions to retain forest within alienated lands are not currently permitted, meaning that within the foreseeable future these critical areas of proboscis monkey habitat will be converted to agriculture. Unless the government takes certain actions, such as amending land laws to allow for land owners to conserve natural habitats, or acquiring alienated lands with proboscis monkey habitat through highly controversial compulsory acquisition, these habitats will undoubtedly be lost, resulting not only in a decline in proboscis monkey numbers but also fragmentation of the remaining population within the Klias Peninsula.

Of equal concern, a further 14% (4,628 ha) of forest habitat (1,182 ha of riverine forest and 3,446 ha of mangrove forest) and 43% (4,117 ha) of degraded forest/swamp habitat are currently classified as Production Forest Reserves (Table 3). All of this riverine forest (1,182 ha) and 885 ha of the mangrove forest noted above are within the Padas Damit Class IV Amenity Forest Reserve, the area where our results revealed the highest numbers of proboscis monkeys. These Amenity Forest Reserves were established mainly to provide recreational opportunities for the general public (Sabah Forestry Enactment, 1968). However, based on follow-up field visits to the Klias Peninsula in 2017/2018 and on examining recent (2019) Google Earth imagery, it was noted that a significant proportion of important proboscis monkey habitat in close proximity or contiguous with Padas Damit Class IV Amenity Forest Reserve has recently been converted to oil palm. Therefore, 80% of riverine, 41% of mangrove forest (i.e., 48% of all forest), and 94% of degraded forest/swamp areas important as proboscis monkey habitat within

alienated lands and Production Forest Reserves in this region are at risk of conversion.

Management implications. Because proboscis monkeys require forests along waterways, continued losses of riverine habitat, especially right up to the river edge, will negatively impact the long-term survival of this endangered species, not only through direct reduction of suitable habitat but also by impeding the movement and dispersal of animals between increasingly fragmented suitable habitat patches (Bernard et al., 2016; Matsuda et al., 2020). Within the Klias Peninsula region, there is a critical need for ongoing monitoring of the proboscis monkey populations, especially near human settlements, as well as monitoring of land-use changes in these priority conservation areas. Furthermore, there is a need to engage with governments to find solutions to conserve remaining habitats. This is also especially important if Sabah plans to sustainably certify its oil palm production state-wide to the Roundtable of Sustainable Palm Oil standards, which require no conversion of key habitat of rare, threatened species such as the proboscis monkey.

One immediate and feasible action we propose to the government is the full protection of proboscis monkey habitat on State Land, which we identified as 1,067 ha of riverine forest, 4,306 ha of mangrove forest, and 1,616 ha of degraded forest/swamp areas (totalling 6,989 ha) (Table 3). This would require stopping the issuance of land titles and gazetting these areas as one of the Protected Area designations. It would also be useful to carry out a study of carrying capacities to evaluate how much of this habitat is required to sustain a stable and viable proboscis monkey population in the Klias Peninsula in the long term.

The Klias Peninsula is a key destination for tourists. Proboscis monkey viewing is a significant part of the local wildlife-based tourism industry, providing livelihoods at the local level and attracting tourists to Sabah at the wider state level. Maintaining viable proboscis monkey populations is hence critical for the state's economy through tourism, which creates a key incentive for the government and local people to protect areas where this species still lives (Lhota et al., 2019). In conclusion, concerted efforts are urgently needed to safeguard almost half of the proboscis monkey habitat within the Klias Peninsula region, so that this endemic, iconic, and endangered primate and the wildlife tourism it generates can be sustained in this region.

ACKNOWLEDGEMENTS

Study data were collected partly through funding granted to Universiti Malaysia Sabah (UMS) via research grant no. GL0067. Field visits to verify land-use changes in the Klias Peninsula in 2017/2018 were funded by UMS through the collaborative research programme no. GKP0012-STWN-2016 awarded to the first author. In this study, the last author was partially financed by JSPS KAKENHI (#19H03308 and #19KK0191) and JSPS Core-to-Core Program, Advance Research Networks (for S. Kohshima). The second author was partially financed by The Woodspring Trust. Permission to conduct the study was kindly granted by the Directors of Sabah Forestry Department and Sabah Wildlife Department. We thank Lucy Wong for assisting with typesetting of the manuscript and Johnny Gisil for identifying the plant species. We sincerely thank the associate editor of RBZ and two anonymous reviewers for their helpful comments and suggestions that have greatly improved the quality and clarity of our paper.

LITERATURE CITED

Abram NK, Meijaard E, Wells JA, Ancrenaz M, Pellier AS, Runting RK, Gaveau D, Wich S, Nardiyono, Tjiu A, Nurcahyo A, Mengersen K & Richardson D (2015) Mapping perceptions of species' threats and population trends to inform conservation efforts: The Bornean orangutan case study. Diversity and Distributions, 21: 487–499.

Abram NK, Xofis P, Tzanopoulos J, MacMillan DC, Ancrenaz M, Chung R, Peter L, Ong R, Lackman I, Goossens B, Ambu L & Knight AT (2014) Synergies for improving oil palm production and forest conservation in floodplain landscapes. PLOS ONE, 9: e95388.

Ancrenaz M, Oram F, Ambu L, Lackman I, Ahmad E, Elahan H, Kler H, Abram NK & Meijaard E (2014) Of Pongo, palms and perceptions: A multidisciplinary assessment of Bornean orang-utans *Pongo pygmaeus* in an oil palm context. Oryx, 49: 465–472.

Ancrenaz M, Oram F, Nardiyono N, Silmi M, Jopony MEM, Voight M, Seaman DJI, Sherman J, Lackman I, Traeholt C, Wich S, Santika T, Struebig MJ & Meijaard E (2021) Importance of small forest fragments in agricultural landscapes for maintaining orangutan metapopulations. Frontiers in Forest and Global Change, 4: 560944.

Beaty TH, Self SG, Liang KY, Connolly MA, Chase GA & Kwiterovich PO (1985) Use of robust variance components models to analyse triglyceride data in families. Annual Human Genetics, 49: 315–328.

Bennett EL, Nyaoi AJ & Sompud J (2000) Saving Borneo's bacon: The sustainability of hunting in Sarawak and Sabah. In: Robinson JG & Bennett EL (eds.) Hunting for Sustainability in Tropical Forests. Columbia University Press, New York, pp. 305–324.

Bennett EL & Sebastian AC (1988) Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in Sarawak. International Journal of Primatology, 9: 233–255.

Bernard H, Bili R, Matsuda I, Hanya G, Wearn OR, Wong A & Ahmad AH (2016) Species richness and distribution of primates in disturbed and converted forest landscapes in northern Borneo. Tropical Conservation Science, 9: 1–11.

Bernard H, Joseph N, Baking EL, Tung SE, Tachiki Y, Oram F, Seelan JSS & Khan FAA (2019b) Animal use of rehabilitated formerly fire damaged peat-swamp forest in western Sabah, Malaysia. Raffles Bulletin of Zoology, 67: 660–670.

Bernard H, Matsuda I, Hanya G & Ahmad AH (2011) Characteristics of night sleeping trees of proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. International Journal of Primatology, 32: 259–267.

Bernard H, Matsuda I, Hanya G, Phua MH, Oram F & Ahmad AH (2019a) Feeding ecology of the proboscis monkey in Sabah, Malaysia, with special reference to plant species-poor forests. In: Nowak K, Barnett AA & Matsuda I (eds.) Primates in Flooded Habitats: Ecology and Conservation. Cambridge University Press, Cambridge, UK, pp. 89–98.

Bernard H & Zulhazman H (2006) Population size and distribution of the proboscis monkey (*Nasalis larvatus*) in the Klias Peninsula, Sabah, Malaysia. Malayan Nature Journal, 59: 1531–1563.

Boonratana R, Cheyne SM, Traeholt C, Nijman V & Supriatna J (2020) *Nasalis larvatus*. The IUCN Red List of Threatened Species 2020: e.T14352A17945165. https://dx.doi.org/10.2305/IUCN.UK.2020-2.RLTS.T14352A17945165.en. (Accessed 22 January 2021).

Chapman CA, Bortolamiol S, Matsuda I, Omeja PA, Paim FP, Reyna-Hurtado R, Sengupta R & Valenta K (2017) Primate population dynamics: Variation in abundance over space and time. Biodiversity and Conservation, 27: 1221–1238.

Chapman CA, Wasserman MD, Gillespie TR, Speirs ML, Lawes MJ, Saj TL & Ziegler TE (2006) Do food availability, parasitism, and stress have synergistic effects on red colobus populations living in forest fragments? American Journal of Physiological Anthropolology, 131: 525–534.

Corlett RT (2007) The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica, 39: 292–303.

Davis JT, Mengersen K, Abram NK, Ancrenaz M, Wells JA & Meijaard E (2013) It's not just conflict that motivates killing of orangutans. PLOS ONE, 8: e75373.

Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A, Nekaris KA, Nijman V, Heymann EW, Lambert JE, Rovero F, Barelli C, Setchell JM, Gillespie TR, Mittermeier RA, Arregoitia LV, de Guinea M, Gouveia S, Dobrovolski R, Shanee S, Shanee N, Boyle SA, Fuentes A, MacKinnon KC, Amato KR, Meyer LA, Wich S, Sussman RW, Pan R, Kone I & Li B (2017) Impending extinction crisis of the world's primates: Why primates matter. Science Advances, 3: e1600946.

Feilen KL & Marshall AJ (2014) Sleeping site selection by proboscis monkeys (*Nasalis larvatus*) in West Kalimantan, Indonesia. American Journal of Primatology, 76: 1127–1139.

Feilen KL & Marshall AJ (2017) Multiple ecological factors influence the location of proboscis monkey (*Nasalis larvatus*) sleeping sites in West Kalimantan, Indonesia. International Journal of Primatology, 38: 448–465.

Fitzherbert EB, Struebig MJ, Morel A, Danielsen F, Bruhl CA, Donald PF & Phalan B (2008) How will oil palm expansion affect biodiversity? Trends in Ecology & Evolution, 23: 538–545.

Gaveau DL, Sloan S, Molidena E, Yaen H, Sheil D, Abram NK, Ancrenaz M, Nasi R, Quinones M, Wielaard N & Meijaard E (2014) Four decades of forest persistence, clearance and logging on Borneo. PLOS ONE, 9: e101654.

Harrison RD (2011) Emptying the forest: Hunting and the extirpation of wildlife from tropical nature reserves. BioScience, 61: 919–924.

Kamlun KU, Arndt RB & Phua MH (2016) Monitoring deforestation in Malaysia between 1985 and 2013: Insight from South-Western Sabah and its protected peat swamp area. Land Use Policy, 57: 418–430.

Koda H, Murai T, Tuuga A, Goossens B, Nathan S, Stark DJ, Ramirez DAR, Sha JCM, Osman I, Sipangkui R, Seino S & Matsuda I (2018) Nasalization by *Nasalis larvatus*: Larger noses audiovisually advertise conspecifics in proboscis monkeys. Science Advances, 4: eaaq0250.

Lhota S, Sha JCM, Bernard H & Matsuda I (2019) Proboscis monkey conservation: Beyond the science. In: Behie AM, Teichroeb JA & Malone NM (eds.) Primate Research and Conservation in the Anthropocene. Cambridge University Press, Cambridge, UK, pp. 182–196.

Matsuda I, Abram NK, Stark DJ, Sha JCM, Ancrenaz M, Goossens B, Lackman I, Tuuga A & Kubo T (2020) Population dynamics of the proboscis monkey *Nasalis larvatus* in the Lower Kinabatangan, Sabah, Borneo, Malaysia. Oryx, 54: 583–590.

Matsuda I, Nakabayashi M, Otani Y, Yap SW, Tuuga A, Wong A, Bernard H, Wich SA & Kubo T (2019) Comparison of plant diversity and phenology of riverine and mangrove forests with those of the dryland forest in Sabah, Borneo, Malaysia. In: Nowak K, Barnett AA & Matsuda I (eds.) Primates in Flooded Habitats: Ecology and Conservation. Cambridge University Press, Cambridge, UK, pp. 15–28.

Matsuda I, Otani Y, Bernard H, Wong A & Tuuga A (2016) Primate survey in a Bornean flooded forest: Evaluation of best approach and best timing. Mammal Study, 41: 101–106.

Matsuda I, Tuuga A, Akiyama Y & Higashi S (2008) Selection of river crossing location and sleeping site by proboscis monkeys (*Nasalis larvatus*) in Sabah, Malaysia. American Journal of Primatology, 70: 1097–1101.

Matsuda I, Tuuga A & Higashi S (2010) Effects of water level on sleeping-site selection and inter-group association in proboscis monkeys: Why do they sleep alone inland on flooded days? Ecological Research, 25: 475–482.

Meijaard E & Nijman V (2000a) Distribution and conservation of the proboscis monkey (*Nasalis larvatus*) in Kalimantan, Indonesia. Biological Conservation, 92: 15–24.

Meijaard E & Nijman V (2000b) The local extinction of the proboscis monkey *Nasalis larvatus* in Pulau Kaget Nature Reserve, Indonesia. Oryx, 34: 66–70.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GA & Kent J (2000) Biodiversity hotspots for conservation priorities. Nature, 403: 853–858.

Phua MH, Tsuyuki S, Lee JS & Sasakawa H (2007) Detection of burned peat swamp forest in a heterogeneous tropical landscape: A case study of the Klias Peninsula, Sabah, Malaysia. Landscape and Urban Planning, 82: 103–116.

R Core Development Team (2019) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org (Accessed 8 September 2018).

Sabah Forestry Enactment (1968) Forest Enactment No. 2 of 1968. Sabah Government Printing, Kota Kinabalu, 49 pp.

Sabah Land Ordinance (1976) Land Ordinance (Sabah Cap. 68). Sabah Government Printing, Kota Kinabalu, 123 pp.

Salter RE, MacKenzie NA, Nightingale N, Aken KM & Chai PKP (1985) Habitat use, ranging behaviour, and food habits of the proboscis monkey, *Nasalis larvatus* (van Wurmb), in Sarawak. Primates, 26: 436–451.

Sha J, Matsuda I & Bernard H (2011) The Natural History of the Proboscis Monkey. Natural History Publications (Borneo), Kota Kinabalu, 126 pp.

Sha JCM, Bernard H & Nathan S (2008) Status and conservation of proboscis monkeys (*Nasalis larvatus*) in Sabah, east Malaysia. Primate Conservation, 23: 107–120.

Sodhi NS, Koh LP, Brook BW & Ng PK (2004) Southeast Asian biodiversity: An impending disaster. Trends in Ecology & Evolution, 19: 654–660.

Stark DJ, Vaughan IP, Evans LJ, Kler H, Goossens B, Pettorelli N & Horning N (2017a) Combining drones and satellite tracking as an effective tool for informing policy change in riparian habitats: A proboscis monkey case study. Remote Sensing in Ecology and Conservation, 4: 44–52.

Stark DJ, Vaughan IP, Saldivar DAR, Nathan SKSS & Goossens B (2017b) Evaluating methods for estimating home ranges using GPS collars: A comparison using proboscis monkeys (*Nasalis larvatus*). PLOS ONE, 12: e0174891.

Thiry V, Stark DJ, Goossens B, Slachmuylder J-L, Vercauteren Drubbel R & Vercauteren M (2016) Use and selection of sleeping sites by proboscis monkeys, *Nasalis larvatus*, along the Kinabatangan River, Sabah, Malaysia. Folia Primatologica, 87: 180–196.

Toulec T, Lhotas S, Soumarova H, Putera AKS & Kustiawan W (2020) Shrimp farms, fire or palm oil? Changing causes of proboscis monkey habitat loss. Global Ecology and Conservation, 21: e00863.

Wich SA, Gaveau D, Abram N, Ancrenaz M, Baccini A, Brend S, Curran L, Delgado RA, Erman A, Fredriksson GM, Goossens B, Husson SJ, Lackman I, Marshall AJ, Naomi A, Molidena E, Nardiyono, Nurcahyo A, Odom K, Panda A, Purnomo, Rafiastanto A, Ratnasari D, Santana AH, Sapari I, van Schaik CP, Sihite J, Spehar J, Santoso E, Suyoko A, Tiju A, Usher G, Atmoko SS, Willems EP & Meijaard E (2012) Understanding the impacts of land-use policies on a threatened species: Is there a future for the Bornean orang-utan? PLOS ONE, 7: e49142.

Woodruff DS (2010) Biogeography and conservation in Southeast Asia: How 2.7 million years of repeated environmental fluctuations affect today's patterns and the future of the remaining refugial-phase biodiversity. Biodiversity and Conservation, 19: 919–941.

Yeager CP (1989) Feeding ecology of the proboscis monkey (*Nasalis larvatus*). International Journal of Primatology, 10: 497–530.

Yeager CP (1990) Proboscis monkey (*Nasalis larvatus*) social organization: Group structure. American Journal of Primatology, 20: 95–106.

Yeager CP (1995) Does intraspecific variation in social systems explain reported differences in the social structure of the proboscis monkey (*Nasalis larvatus*)? Primates, 36: 575–582.