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RESEARCH ARTICLE

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A decade of proboscis monkey (*Nasalis larvatus*) population monitoring in Balikpapan Bay: Confronting predictions with empirical data

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Abstract

Systematic and well-structured monitoring is essential for taxa with high extinction risk such as primates. Endangered proboscis monkeys *Nasalis larvatus* are endemic to Borneo, where they are found scattered across lowland habitats of the island, which are under strong anthropogenic pressure. A large population of proboscis monkeys in Balikpapan Bay, Indonesian Borneo, was predicted to decline due to the ongoing habitat loss and degradation, notably because of forest fires. We examined changes in the number and composition of groups of a part of this population from 2007 to 2017, which included a period of forest fires linked to the El Niño–Southern Oscillation events. We conducted a census from a boat; attempting to locate all proboscis monkey groups within the Balikpapan City administrative area in 2007, 2012, and 2017. During the most recent census, we observed a total number of 60 proboscis monkey groups in two subpopulations. The population density was 1.14 group per km^2 of suitable habitat. Contrary to previously published predictions, we did not find evidence of a population decline. Contrary to predictions, the 2015 El Niño induced fires impacted mainly forests on ridges and slopes, thus affecting only a small part of the proboscis monkey habitat located close to rivers and mangrove swamps. However, the increasing population density of monkeys, coupled with ongoing habitat degradation and habitat loss in one of the subpopulations, suggests that proboscis monkey population in Balikpapan Bay may be approaching a limit of resilience to habitat changes. In case it proves infeasible to census all individuals in the whole population, we recommend using a group-level census, connected with systematic group counts to obtain a reasonably precise proboscis monkey population size estimate.

KEYWORDS

Borneo, group composition, *Nasalis larvatus*, population census, population dynamics

1 | INTRODUCTION

Over the last few decades, it has been shown that longer-term studies of wildlife populations are of increasing scientific and conservation management importance (Kappeler et al., 2012; Margalida, 2017; Pelton & Van Manen, 1996). This is particularly true of taxa with long life spans such as many species of primates, which require several years of research to adequately document their life histories (Chapman et al., 2017). Several long-term research projects have provided empirical data on primate population dynamics and demography over extensive periods, for example, chimpanzees *Pan troglodytes* (Goodall, 1983), white-faced capuchin monkeys *Cebus imitator* (Hogan et al., 2019), northern muriquis *Brachyteles hypoxanthus* (Strier, 2021), or several primate taxa in Kibale National Park, Uganda (Lwanga et al., 2011). However, long-term data are still lacking for the majority of primate species and populations. Given that over 60% of primate species are threatened with extinction (Estrada et al., 2017), it is important to acquire and publish more long-term population data that will contribute to our understanding of population dynamics.

Endemic to the island of Borneo, proboscis monkeys *Nasalis larvatus* primarily live in seasonally flooded lowland habitats, such as mangrove and riparian forests (Kawabe & Mano, 1972; Meijaard & Nijman, 2000a; Salter et al., 1985), where they occur at very different densities both within and between habitat types (riparian 25.5–62.6 individuals/km^2; mixed forest types 4.4–6.9 individuals/km^2; and mangrove 6.6–35.1 individuals/km^2, Table 1). They typically choose sleeping sites close to the edge of open water, making the species relatively easy to survey from boats (Boonratana, 1993; Kern, 1964; Matsuda et al., 2011; Yeager, 1989). Individual groups scatter to the surrounding forest during the day to rest or forage young leaves and young fruits (Matsuda et al., 2009; Yeager, 1989). Proboscis monkeys typically form nonterritorial one-male units (one adult male and several females with offspring; OMUs) or all-male units (AMU) (Bennett & Sebastian, 1988; Yeager, 1990a), and both females and males disperse (Matsuda et al., 2015; Murai et al., 2007; Yeager, 1990a). These groups tend to congregate at sleeping sites. These associations are sometimes described as a secondary level of social organization (Yeager, 1991). These loose congregations usually split in the morning into individual groups to forage some distance from the riverbanks. The major threats to proboscis monkeys include loss of mangrove and riparian forest (mainly due to conversion into aquaculture, agriculture, or destruction due to forest fires), habitat fragmentation, and also hunting locally (Boonratana, 2013; Meijaard & Nijman, 2000a; Salter & MacKenzie, 1985; Sha et al., 2008), yet the impact on individual populations remains largely undocumented. Moreover, accurate population size data are scarce.

Population size estimates for the four major political divisions of Borneo (i.e., the Malaysian states of Sabah and Sarawak, Indonesian Kalimantan, and Brunei Darussalam) differ widely, and many are based on surveys and extrapolations from over a decade ago: Sabah (5907: Sha et al., 2008), Sarawak (fewer than 1000 individuals: Bennett, 1988; 9586: Laman & Aziz, 2019), Brunei (420: Salter & MacKenzie, 1985), Kalimantan (~8000–12,000: Meijaard & Nijman, 2000a; 9200: Manansang et al., 2004). The accuracy of those estimates could be biased. The possible causes of overestimation are

TABLE 1 Comparison of studies concerning proboscis monkey (*Nasalis larvatus*) population density

Location	Forest type	Density (individuals/km^2)	Authors
Tanjung Puting (C Kalimantan)	Riparian	62.6	Yeager (1989)
Menanggul River (Sabah)[a]	Riparian	28.8/29.8/34.0	Murai (2004)/Matsuda (2008)/Boonratana (1993)
Rawa Galam (S Kalimantan)	Riparian	28.3	Iskandar et al. (2017)
Tanjung Belimbing (W Kalimantan)	Riparian	25.5	Selpa et al. (2019)
Kinabatangan Floodplain (Sabah)[a]	Mixed	6.9/7.9	Goossens et al. (2002)/Sha et al. (2008)
Samunsam Wildlife Sanctuary (Sarawak)	Mixed	5.9	Bennett and Sebastian (1988)
Klias Peninsula (Sabah)	Mixed	4.4	Bernard and Zulhazman (2006)
Merah River (Sabah)	Mangrove	10.0	Boonratana (1993)
Bako (Sarawak)	Mangrove	24.1	Salter and MacKenzie (1985)
Berau Delta (S Kalimantan)	Mangrove	6.6	Atmoko et al. (2021)
Pemaluan River (E Kalimantan)[b]	Mangrove	7.5	Lhota and Gokil (2011, unpubl. data)
Hutan Kariangau[b]	Manhhgrove	6.9	Toulec et al. (this study)
Somber River[b]	Mangrove	51.5	Toulec et al. (this study)

Note: The general method was boat surveys, but varied in survey effort and group classification.

Riparian habitats are forests along freshwater streams. Mangrove habitats are found in intertidal zones flooded with saltwater or brackish water. Mixed habitat is a combination of riparian and mangrove forest.

[a]Locality around the Kinabatangan River.

[b]Locality within Balikpapan Bay.

double counts of groups or, as in the case of Laman and Aziz (2019), extrapolation of the occurrence and abundance of the species from the extent of forest types, which may not precisely correspond to the species-specific habitat selection. Underestimation is mostly associated with surveying extensive areas too quickly and missing some groups.

Proboscis monkeys are classified by IUCN as "Endangered" with a decreasing population trend (Boonratana et al., 2020); however, the trend remains poorly documented for most populations. Long-term population monitoring programs for proboscis monkeys have been reported only for the Lower Kinabatangan floodplain (Matsuda et al., 2020) and for Klias Peninsula (Bernard et al., 2021) in Sabah. Using a population modeling approach and based on data collected more than a decade ago, Stark et al. (2012) predicted Kinabatangan's population should remain stable in terms of a number of individuals until the end of their 50-year modeling period. Accordingly, Matsuda et al. (2020), based on empirical data, found a relatively unchanged number of groups between 2004 and 2014, although they documented a decline in group size during this period.

Balikpapan Bay, on the east coast of Indonesian Borneo, covers 203 km^2 of proboscis monkey habitat and combines coastal mangroves and an adjoining belt of secondary coastal forests (Toulec et al., 2020). This population was roughly described to contain 100–1000 individuals based on a limited number of surveys and available habitats (Meijaard & Nijman, 2000a). When Stark et al. (2012) reassessed this population, it increased to 1400 individuals based on more extensive surveys and a better understanding of the species' distribution.

Stark et al. (2012) applied a population viability analysis (PVA) to predict the future dynamics of the proboscis monkey population in Balikpapan Bay. PVA models have been deployed as a technique to gain better insight into the conservation status and likelihood of persistence of a target population (Boyce, 1992). The baseline scenario of the model used by Stark et al. (2012) predicted a rapid decline of the proboscis monkey population in Balikpapan Bay, with a non-zero risk of extinction in a mean time frame of 44 years, because of excessive habitat loss. Stark et al. (2012) suggested that the total prevention of forest fires was the most promising management strategy to alter predicted population decline in Balikpapan Bay. They predicted that the population would stabilize after a slight initial drop during the first 10 years. Hunting was evaluated as a negligible threat in Balikpapan Bay and did not play a role in their model.

Forest fires on Borneo are strongly connected to El Niño–Southern Oscillation (ENSO) events, which causes extremely dry conditions. Their impact has been increasing since 1980s (Fredriksson, 2002; Yeager & Fredriksson, 1998). In September and October 2015, another ENSO struck Southeast Asia, which resulted in a highly flammable environment (Tacconi, 2016). This resulted in severe forest fires, including damage to the Sungai Wain Protection Forest (Pro Natura Foundation, 2016) that adjoins Balikpapan Bay and that forms part of the Tengah River population. About the same time, several unprotected coastal forested areas were damaged by deliberate fires caused by gangs of land speculators (Lhota, 2016, unpubl. obs.). However, a detailed analysis of habitat changes revealed that oil palm plantations, industrial development, and aquaculture were the main drivers of deforestation in Balikpapan Bay and that forest fires damaged proboscis monkey habitat only marginally due to the relatively humid character of their riverside habitat (Toulec et al., 2020).

In this study, we assessed changes in proboscis monkey population size in Balikpapan Bay from 2007 until 2017. Stark et al. (2012) used data collected in 2007 to predict the future development of Balikpapan Bay's population. The subsequent study periods (2012 and 2017) included the 2015 forest fires event. According to the baseline scenario of the PVA model (Stark et al., 2012), we expected the population to decline after the fires. However, Toulec et al. (2020) found a slow but constant rate of habitat loss during this period, with little effect of forest fires on the relatively humid proboscis monkey habitat. On the basis of this finding, we expected that the local population of proboscis monkeys would remain stable. We monitored the population at the group level, as we could not count the size of most of the groups; a possible error in estimating average group size based on our sample would be multiplied when converting the number of groups to the total number of individuals. We also investigated the size and age–sex composition of groups and differences between population dynamics in two distinct subpopulations within the study area. Understanding the size and dynamics of the Balikpapan Bay population may provide valuable insight into the conservation value of other proboscis monkey populations that inhabit a similar landscape (e.g., populations in Adang, Apar, or Sangkulirang Bays, East Kalimantan), and, therefore, may help to prioritize efforts to protect the whole taxon. We also offer some suggestions on suitable and promising methods of surveying and censusing proboscis monkeys, and estimating their population size in future research.

2 | METHODS

2.1 | Ethics statement

We did not handle any animals in our study, and our research adhered to the American Society of Primatologists principles for the ethical treatment of nonhuman primates. The research was approved by the Indonesian Institute of Sciences in 2007 (No. 6010/SU/KS/2007) and by the Ministry of Research and Technology of Indonesia in 2012 (No. 118/SIP/FRP/SM/V/2012) and 2017 (No. 895/FRP/E5/Dit.KI/V/2017).

2.2 | Study area

Balikpapan Bay is located on the coast of East Kalimantan, one of five Indonesian provinces on the Island of Borneo (1° 8′ S, 116° 45′ E). Administratively it is situated largely in the district of Penajam Paser Utara (PPU) Regency with a smaller section in the southeast being

part of Balikpapan City. The coast of Balikpapan Bay is not part of any protected area, although one of its upper watershed areas is protected at the provincial level as the Sungai Wain Protection Forest (Figure 1).

Most of the coast is covered with mangroves, which are located along with more than 50 small and predominantly tidal river systems within Balikpapan Bay. The extent of alluvial and freshwater swamp forest in this area is negligible. Among those river systems, 12 are located within the Balikpapan City administrative area. These rivers are the focus of the present study and range from 0.6 to 11.2 km in length along the main river (Figure 1, Table S1). All river systems have small watersheds and temporary flooding had only a minor effect on the water level compared to daily tidal changes. There is no prolonged seasonal flooding in any of these rivers. The southern part of the study area (Teluk Kariangau), which is adjacent to the urban area of Balikpapan, contains the following rivers: Wain, Keminting, Cina, Paka Dua, Getah, and Somber. The northern part of the study area (Hutan Kariangau) contains rivers Puda, Tengah, Berenga, Tempadung, Baruangin and Kemantis (Figure 1, Table S1).

2.3 | Censusing number of groups

Proboscis monkeys show a strong tendency to return to their sleeping sites located along the water's edge (known as riverine refuging behavior by Matsuda et al., 2011). Their behavior, combined with the inaccessibility of their mangrove habitat on foot, makes boat trips along with the sleeping sites an optimal method for surveying or censusing this species. Boat surveys have been applied in numerous previous studies (Goossens et al., 2002; Matsuda et al., 2020; Meijaard & Nijman, 2000a; Salter et al., 1985; Sha et al., 2008). The common approach of a boat survey is to survey a segment of the river only once rather than repeatedly, to estimate the number of groups present within the particular area.

We adopted an alternative approach. Similar to Bennett and Sebastian (1988), we aimed to locate all proboscis monkey groups in the river systems of Balikpapan City administrative area. Therefore, we refer to our method as a group-level census. A census of a particular river system consisted of several consecutive sessions (maximum of nine per river system) until we were convinced that all groups have been located, using contextual cues (group position and direction of progression, its approximate size, distinctive individuals). A session refers to two boat trips: one in the late afternoon (starting ~7:00 h until dusk) and another early the following morning (from dawn until ~08:00 h), before the monkeys leave the vicinity of their sleeping sites. Most data were collected during the evening boat trips, while morning boat trips served mainly for verification. A boat trip was only canceled when our boatman could not guarantee the safety of the team due to unfavorable weather conditions. The average distance in 2017 was 6.36 km per boat trip (±SE: 0.29), and the speed of the boat was kept below 9 km/h when searching for monkeys.

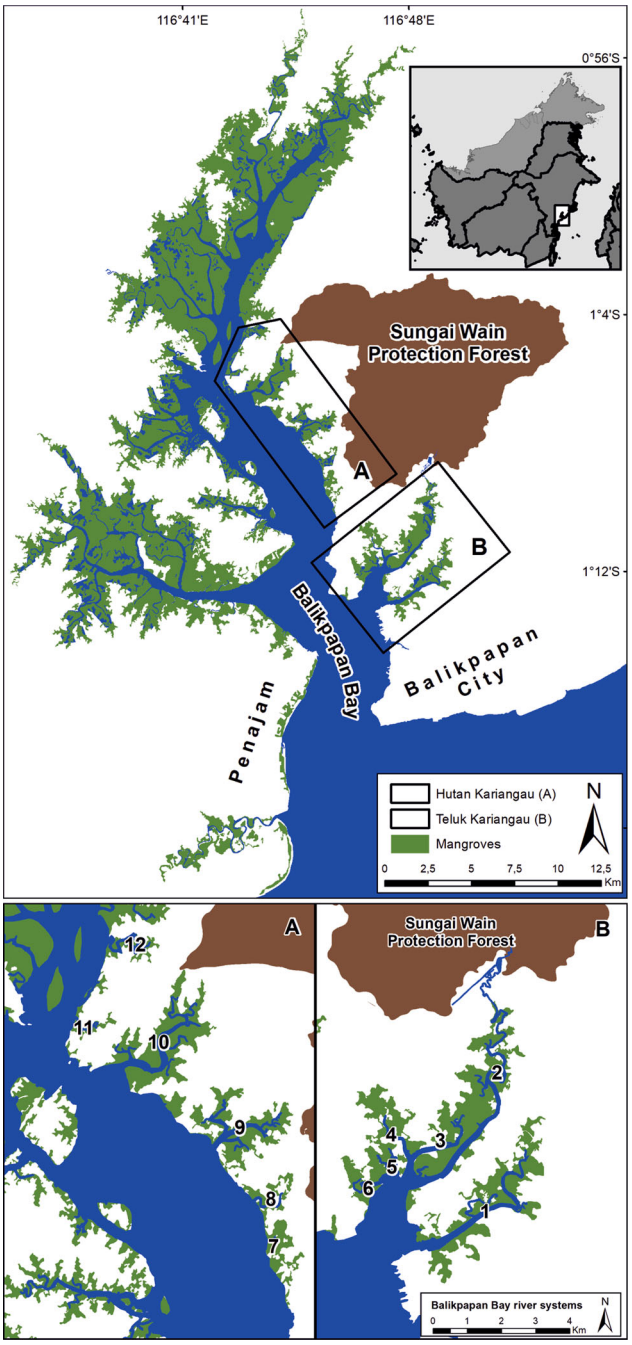

FIGURE 1 Balikpapan Bay, Indonesia, with the extent of mangroves, representing core areas of proboscis monkey (*Nasalis larvatus*) habitat. The location of two study sites within Balikpapan City administrative area, A: Hutan Kariangau, B: Teluk Kariangau. Detailed river systems within Balikpapan City administrative area. Hutan Kariangau (A): Puda (7), Tengah (8), Berenga (9), Tempadung (10), Baruangin, (11) and Kemantis (12). Teluk Kariangau (B): Somber (1), Wain (2), Keminting (3), Cina (4), Paka Dua (5), and Getah (6)

We started our observations on proboscis monkeys in Balikpapan Bay and adjacent Sungai Wain Protected Forest in 1999 (Vincent Nijman) and 2005 (Stanislav Lhota). Censuses in 2007, 2012, and 2017 were conducted by different observers but were highly

coordinated. Stanislav Lhota made the first proboscis monkey population census during November and December 2007. He was present in the area during the two following censuses and participated in training the other two observers, boatmen, and their field assistants. Katherine Scott replicated the census in Balikpapan City administrative area from April to June 2012. Finally, Tadeáš Toulec and Alexander K. S. Putera conducted the census in May and June 2017. Local students and representatives of local NGOs and government officers were invited to join the census occasionally to build local capacity and share their experiences; their presence did not affect the detectability of the monkeys.

For this study, we used one small boat with a 24 hp outboard motor, similar to the boats that are regularly used by local fishermen. The monkeys are usually habituated to this type of boat; however, they become alert and tend to retreat further to the forest once the boat stops or cruises too close. Therefore, we kept a minimum distance of 20 m from the monkeys during observations and used binoculars for individual identification. The only exception in methodology was on the edge of the Sungai Wain Protection Forest (Figure 1), as the water reservoir (with sleeping sites close to its banks) is not accessible by boat. However, due to maintenance of the water reservoir and its banks, accessibility and visibility are sufficient and counting could be done on foot.

Following each boat trip (or a walk along the water reservoir), we recorded all observations of groups on a map. To avoid double-counting of the same group during the subsequent boat trips to the same area, we kept detailed notes on contextual cues which enabled temporary identification of individual groups. Groups were initially divided by a group type (OMU or AMU) adding information about group composition, overall group size, individuals with identifying features (Table S2), the presence and number of dark-colored infants (OMUs only), and the direction of group progression. We tried to track the identity of all observed groups as they changed their sleeping sites on subsequent nights. We occasionally confirmed the presence of an unseen group hidden in the forest by the characteristic adult male vocalization and the noise of a group movement.

Several groups of OMUs and AMUs can associate with sleeping trees along the same riverbank. Although the groups do not normally mix in the same trees, they can still be very close to one another, making it difficult to differentiate among groups. To ensure that we counted the number of groups correctly we focused on counting the highly conspicuous adult males. AMUs may, however, contain more than one fully-grown adult male. Furthermore, sometimes the adult males enter the sleeping trees relatively late or stay low in trees compared to the rest of the group and can be missed. The snarl (bray) calls and other age-and-sex-specific vocalizations can also help locate the fully-grown adult males. Other group members produce these calls only rarely (Röper et al., 2014).

Having completed the census for one river system, we compiled information from the series of maps into a composite map of ranging patterns of all observed groups and established the total number of groups and individuals in that river system. We then proceeded to census the next nearest river system. When mapping group movements, we also considered the possibility that the groups may move not only within but also between neighboring river systems.

2.4 | Determining group size and composition

Most of the time, it was impossible to see and count all members of the group during the evening and morning census. While we maximized our effort to census all groups, group size and age–sex composition could only be determined for a subset of these groups. These data were only collected in 2007 and 2017, and the methods to obtain the size and age-sex composition differed between these two periods. Stanislav Lhota recorded group size and composition opportunistically during the 2007 census, whenever he felt that the visibility was good and that all group members may be seen. In contrast, Tadeáš Toulec and Alexander K. S. Putera devoted the second phase of the field research (July 2017) to systematic group counts where they counted a subset of proboscis monkey groups located along selected rivers that represented a smaller part of the total census area. The systematic group counts focused on repeated boat trips along with several selected river systems (Kemantis, Tempadung, Tengah Rivers, and the middle part of Somber River). All groups were counted repeatedly on several subsequent days until Tadeáš Toulec and Alexander K. S. Putera were confident that all group members were included. When counting group members, we referred to the following age–sex categories: adult male and female, subadult male, juvenile male and female, infant (Table S2).

During the fieldwork, we recognized that the Teluk Kariangau subpopulation (in the southern part of the study area and near urban areas) may be rather aberrant and unstable and may not properly represent the whole Balikpapan Bay population. Therefore, we have decided to compare the unpublished data on group sizes and composition collected in the PPU Regency, outside the administrative area of Balikpapan City, using the same methods of systematic group counts. Stanislav Lhota collected data on the Pemaluan River in 2011 (seven OMUs, one AMU) and on two tributaries of Riko Mati River in 2020 (eight OMUs, two AMUs), in the northwestern and western part of Balikpapan Bay.

2.5 | Estimating population density

We measured and calculated the available habitat of two sections of the Balikpapan City administrative area from satellite imagery in ArcGIS 10.6. We adopted the approach of Toulec et al. (2020) using all mangroves and 120 m of suitable adjoining terrestrial forest (excluding patches of urbanized areas, oil palm plantations, grasslands, etc.) as proboscis monkey habitat. This 120-m belt represented the maximum distance we observed proboscis monkey outside mangroves in Balikpapan Bay. We used the following formula to determine group density

$$\text{population density} = \frac{\text{number of groups or individuals}}{\text{extent of habitat}(\text{km}^2)}.$$

The population size of the entire Balikpapan Bay was then estimated by multiplying population density by the total area of proboscis monkey habitat. We are aware of the heterogeneity of habitat and proboscis monkey distribution in Balikpapan Bay, and we attempted to cover the largest area possible for the census (26.35 km^2) to enhance the representativeness of our estimate. The estimate represents the closest available approximation of real population size. We used χ^2-tests to evaluate the statistical significance of population change between three years. We performed simple linear regression to find out whether the difference in the number of groups observed in individual river systems during the first (2007) and the final (2017) census resulted from different census efforts measured as the number of sessions and the length of rivers that were traveled. We used *t*-tests to compare changes in the size of OMUs and AMUs and to find out similarities between subpopulations. We calculated the encounter rate as the number of groups observed per km of riverbank censused.

3 | RESULTS

3.1 | Group abundance and proportion of AMUs

We conducted a total number of 32, 43, and 38 sessions (evening and subsequent morning boat trips) in 2007, 2012, and 2017, respectively. Proboscis monkey groups encountered on individual river systems and throughout the sampling period could be seen in Figure 2 and Table 2. In addition, we encountered three solitary individuals in 2012 and one solitary male in 2017. Using 2007 as the baseline, the total number of groups we recorded over the 10-year period increased by 17.7%, but this was not statistically significant ($\chi^2 = 0.68$, $df = 2$, $p = 0.712$).

We calculated the difference in the number of groups encountered for each of the 12 river systems, and the difference in the number of sessions, between the first (2007) and last (2017) censuses (Table S1). There was no significant effect on the difference of census effort (number of sessions/length of rivers traveled) on the difference of the number of encountered groups ($n = 12$ rivers, $r = 0.16$, $p = 0.62$). When we pooled the data for both censuses, there was a significant positive relationship between the number of sessions in a river system, and the number of the observed groups ($n = 24$, $r = 0.48$, $p = 0.02$). The encounter rate was, however, not related to the number of sessions ($n = 24$, $r = 0.01$, $p = 0.96$), suggesting that we terminated the census right around the time when we already detected all present groups (Table S1). The number of observers on the boat was not consistent across seasons; there were only two observers in 2007 and 2012, compared to up to five in 2017. However, the number of groups encountered during the first two censuses is proportional to the number of groups encountered during the final census ($\chi^2 = 0.41$, $df = 1$, $p = 0.52$). Therefore, the additional observers on the boat do not seem to have increased the ability of the team to locate the groups.

The number of proboscis monkey groups in most watersheds fluctuated over the three periods, but not in a consistent or predictable manner (Figure 2). OMUs were present at least once on every river, contrary to AMUs, which were often absent in one in every three censuses. The only two watersheds where AMUs were never encountered during the observations were Berenga and Puda.

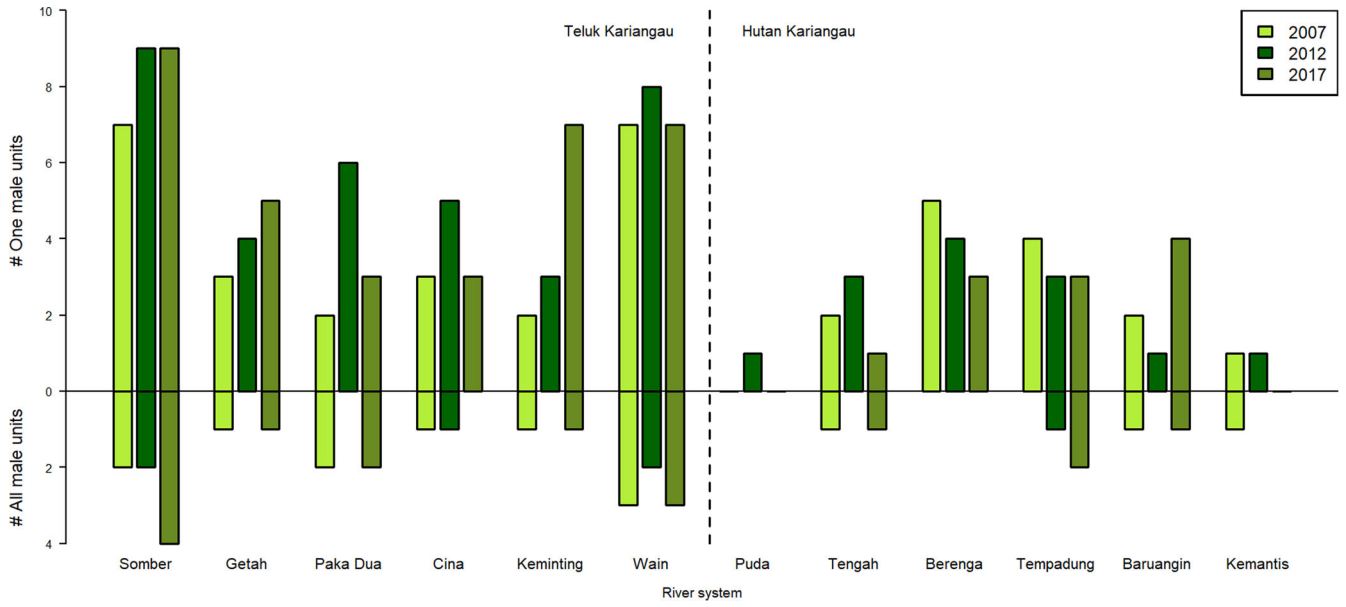

FIGURE 2 Proboscis monkey group counts in all 12 river systems within Balikpapan City administrative area, over a 10-year period. Emphasis on two different group types of proboscis monkey—all-male unit and one-male unit

TABLE 2 Group counts of wild proboscis monkey (*Nasalis larvatus*) in three census years in Balikpapan Bay administrative area, Indonesia, including the total number of one-male units (OMUs) and all-male units (AMUs) in each river system and the total number of groups observed per census year

River system	2007		2012		2017	
	# OMU	# AMU	# OMU	# AMU	# OMU	# AMU
Teluk Kariangau						
Somber	7	2	9	2	9	4
Getah	3	1	4	0	5	1
Paka Dua	2	2	6	0	3	2
Cina	3	1	5	1	3	0
Keminting	2	1	3	0	7	1
Wain	7	3	8	2	7	3
Total	24	10	35	5	34	11
Total subpopulation	34		40		45	
Hutan Kariangau						
Puda	0	0	1	0	0	0
Tengah	2	1	3	0	1	1
Berenga	5	0	4	0	3	0
Tempadung	4	0	3	1	3	2
Baruangin	2	1	1	0	4	1
Kemantis	1	1	1	0	0	0
Total	14	3	13	1	11	4
Total subpopulation	17		14		15	
Total: Balikpapan City administrative area	38	13	48	6	45	15
	51		54		60	

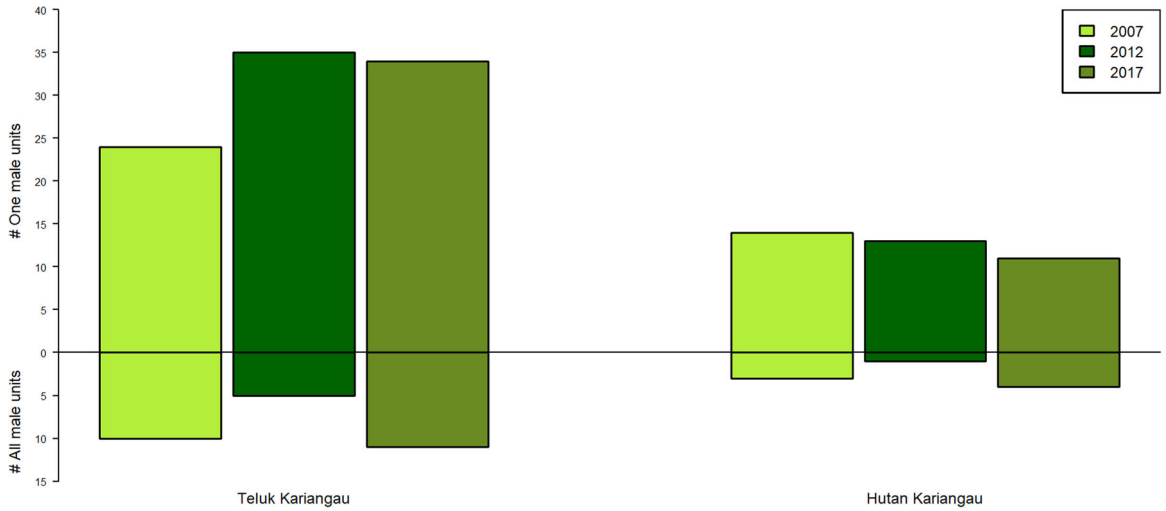

FIGURE 3 Proboscis monkey subpopulation group counts in Balikpapan City administrative area, over a 10-year period, divided by two different group types.

3.2 | Subpopulation dynamics

When considering both subpopulations separately, the changes in group numbers were relatively more pronounced compared to the overall change, with different tendencies in each subpopulation. In Teluk Kariangau subpopulation, group numbers increased gradually by 17.7% (2007–2012) and by another 12.5% until 2017, but it did not reach statistical significance ($\chi^2 = 0.47$, $df = 2$, $p = 0.791$).

TABLE 3 Composition of encountered groups during opportunistic group counts of proboscis monkey (*Nasalis larvatus*) in 2007

One-male unit	# Adult males	# Adult females	# Subadult males	# Juveniles	# Infants	Total
Hutan Kariangau 2007 (n = 4)						
Mean ± SE	1.00 ± 0.00	5.00 ± 1.87	0.00 ± 0.00	1.00 ± 0.00	4.00 ± 2.55	11.00 ± 4.30
Range		3–8			0–7	5–17
Teluk Kariangau 2007 (n = 13)						
Mean ± SE	1.00 ± 0.00	3.54 ± 0.33	0.08 ± 0.08	0.62 ± 0.14	2.38 ± 0.38	7.62 ± 0.76
Range		3–7	0–1	0–1	0–5	5–14
All-male unit						
Hutan Kariangau 2007 (n = 2)						
Mean ± SE	1.50 ± 0.50	0.50 ± 0.50	0.00 ± 0.00	0.50 ± 0.50	0.00 ± 0.00	2.50 ± 0.00
Range	1–2	0–1		0–1		2–3
Teluk Kariangau 2007 (n = 7)						
Mean ± SE	2.29 ± 0.45	0.00 ± 0.00	1.14 ± 0.64	1.57 ± 1.50	0.00 ± 0.00	5.00 ± 1.69
Range	2–3		0–2	0–4		3–8

Note: Only groups with confirmed sex-age classes were sorted into categories (Table S2), n represents the number of censused groups.

The Hutan Kariangau subpopulation count fluctuated, declining after the first 5 years by 17.7% and then increasing by 7.1% from 2012 to 2017 (Figure 3). Again, this was not statistically significant ($\chi^2 = 0.86$, $df = 2$, $p = 0.651$).

3.3 | Size of OMUs and AMUs

During the 2007 census, we opportunistically recorded group size and composition for 17 OMUs (44.7% of OMUs encountered) and 7 AMUs (53.9% of encountered male groups) (Table 3). Systematic group counts in 2017 enabled us to count all members of all groups on three selected rivers in Hutan Kariangau and in the middle part of the Somber River (total 12 OMUs, 7 AMUs) (Table 4).

Overall, OMUs were larger than AMUs in both subpopulations and in the Pemaluan River, through all censuses (Tables 3 and 4); Riko Mati River was, however, exceptional with one considerably larger AMU of 16 individuals. OMUs also significantly increased in size from 2007 to 2017 ($t = 2.90$, $df = 26$, $p = 0.01$). This increase was, however, only evident in Teluk Kariangau, both in terms of OMU ($t = 5.07$, $df = 17$, $p = 0.0001$) and AMU ($t = 3.01$, $df = 8$, $p = 0.02$). In contrast, Hutan Kariangau subpopulation OMUs ($t = 0.29$, $df = 6$, $p = 0.78$) and AMUs ($t = 0.44$, $df = 4$, $p = 0.68$) did not change significantly in size. Teluk Kariangau's OMUs in 2017 represent the largest groups censused. The smallest mean group size was Hutan Kariangau's AMU in 2017 (mean 3.50 ± SE 1.50; Table 4).

3.4 | Age–sex composition

We only observed a single adult male and usually no subadult males in OMUs (Tables 3 and 4). A subadult male was only observed once in an OMU within the Balikpapan City administrative area (with one additional observation on the Pemaluan River) (Table 5). An adult female appeared only once in an AMU (we decided not to classify this as a different type of group). No infants were seen in AMUs; however, juveniles were commonly seen, notably in Teluk Kariangau in 2017, and some of them were very young. As many as three adult males may have been residing in an AMU, but we have also observed AMUs without adult males (Table 4). The proportion of adult males residing in AMUs compared to those residing in OMUs decreased in the 10-year period in both subpopulations, but the change was most obvious in Teluk Kariangau, where it corresponds with an increasing number of OMU (Table 2) and decreasing average number of adult males in AMU of known composition (Table 5).

An additional difference in the dynamics of the two subpopulations is evidenced by the proportion of adult females to adult males. This ratio had increased largely in 2017 in Teluk Kariangau, whereas it decreased in Hutan Kariangau. Furthermore, the ratio of immatures to adult females increased in both subpopulations (Table 5).

3.5 | Population density and estimating total population size

The estimate of proboscis monkey group density based on habitat size for each period, gradually increased in Teluk Kariangau, with a peak in 2017 (3.79 group/km^2) and fluctuated in much lower values in Hutan Kariangau (Table 6). The average group density during the whole period was 3.00 groups/km^2 in Teluk Kariangau and 1.11 groups/km^2 in Hutan Kariangau. We also compared data for both subpopulations with data collected in other rivers of Balikpapan Bay. The average OMU size of Pemaluan River (mean 10.86 ± SE 1.75) and Riko Mati River (8.75 ± SE 1.73) resembled the situation in

TABLE 4 Composition of encountered groups during systematic group counts

One-male unit	# Adult males	# Adult females	# Subadult males	# Juveniles	# Infants	Total
Hutan Kariangau 2017 (*n* = 5)						
Mean ± SE	1.00 ± 0.00	4.20 ± 1.20	0.00 ± 0.00	1.40 ± 040	3.00 ± 0.63	9.60 ± 1.89
Range		2–8		0–2	2–5	5–15
Teluk Kariangau 2017 (*n* = 6)						
Mean ± SE	1.00 ± 0.00	6.67 ± 1.02	0.00 ± 0.00	3.17 ± 0.79	6.33 ± 0.71	17.17 ± 2.30
Range		4–10		1–6	4–9	11–26
Pemaluan River 2011 (*n* = 7)						
Mean ± SE	1.00 ± 0.00	4.71 ± 0.87	0.29 ± 0.18	1.43 ± 0.37	3.43 ± 0.53	10.86 ± 1.75
Range		2–9	0–1	0–3	2–6	5–20
Riko Mati River 2020 (*n* = 8)						
Mean ± SE	1.13 ± 0.13	3.75 ± 0.65	0.00 ± 0.00	1.13 ± 0.61	2.75 ± 0.53	8.75 ± 1.73
Range	1–2	1–7		0–5	1–5	4–19
All-male unit (AMU)						
Hutan Kariangau 2017 (*n* = 4)						
Mean ± SE	0.75 ± 0.25	0.00 ± 0.00	1.75 ± 0.48	1.00 ± 1	0.00 ± 0.00	3.50 ± 1.50
Range	0–1		1–3	0–4		2–8
Teluk Kariangau 2017 (*n* = 3)						
Mean ± SE	0.33 ± 0.33	0.00 ± 0.00	2.00 ± 0.58	6.00 ± 0.58	0.00 ± 0.00	8.33 ± 0.33
Range	0–1		1–3	5–7		8–9
Pemaluan River 2011 (*n* = 1)						
Mean ± SE	1	0	2	1	0	4
Range						
Riko Mati River 2020 (*n* = 2)						
Mean ± SE	2.38 ± 1.62	0.50 ± 0.50	2.27 ± 0.27	4.50 ± 4.50	0.00 ± 0.00	9.65 ± 6.36
Range	0.76[a]–4	0–1	2–2.53[a]	0–9		3.29[a]–16

Note: Two additional river systems in Penajam Paser Utara Regency (Pemaluan River and Riko Mati River) are included for comparison by Lhota and Gokil (2011, unpubl. data); Darman et al. (2020, unpubl. data), *n* represents the number of censused groups.

[a]Composition of one of the AMUs on the Riko Mati River changed during the period of the census, hence the range of group size is represented as an average in this group.

Hutan Kariangau in 2007 (12.14 ± SE 1.60; $t = 0.54$, $df = 12$, $p = 0.599$) and differed significantly from Teluk Kariangau in 2017 (17.17 ± SE 2.30; $t = 2.22$, $df = 11$, $p = 0.049$). Therefore, we provisionally chose Hutan Kariangau as a reference subpopulation for the whole Balikpapan Bay. This resulted in a total estimate of 2603 (2007), 2165 (2012), and 1801 (2017) proboscis monkeys in Balikpapan Bay.

4 | DISCUSSION

The number of proboscis monkey groups encountered in three censuses over a decade in Balikpapan Bay increased from 51 (2007) to 54 (2012) and 60 (2017) but the change was not statistically significant. We interpret this as a stable or possibly increasing population. Some fluctuation in the number of recorded individuals encountered during the survey may be inherent to any sampling and even census attempt. It has also been observed during repeated surveys in Lower Kinabatangan (Matsuda et al., 2020, fig. 2). Fluctuation in the number of groups and/or individuals may reflect changes in population size, group structure (such as splits or fusions), ranging patterns, as well as sampling error. These data, therefore, need to be treated with caution; they should only be interpreted as showing a population change if there is a significant and consistent trend over several consecutive periods. In our case, it is reasonable to conclude that the proboscis monkey population in Balikpapan Bay does not show a decline, which was predicted by Stark et al. (2012). The observed stability corresponds with the findings of Toulec et al. (2020), who estimated the annual rate of the proboscis monkey

TABLE 5 Indices of sex and age composition for four proboscis monkey subpopulations in Balikpapan Bay

	Teluk Kariangau (*n*)	2007 2017	Hutan Kariangau (*n*)	2007 2017	Pemaluan River 2011 (*n*)	Riko Mati River 2020 (*n*)
Adult males in OMU/all adult males in subpopulation	0.42 (13) 0.86 (6)		0.57 (4) 0.63 (5)		0.88 (7)	0.65 (9)
Subadult males in OMU/all subadult males in subpopulation	0.11 (1) 0.00 (0)		0.00 (0) 0.00 (0)		0.50 (2)	0.00 (0)
Adult females/adult males in OMU	3.54 (46) 6.67 (40)		5.00 (20) 4.20 (21)		4.71 (33)	3.33 (30)
Adult females/adult males in subpopulation	1.48 (46) 5.71 (40)		3.00 (21) 2.63 (21)		4.13 (33)	2.25 (31)
Immatures/adult females ratio in OMU	0.85 (39) 1.43 (57)		1.00 (20) 1.05 (22)		1.03 (34)	1.03 (31)
Immatures/adult females ratio in subpopulation	1.09 (50) 1.88 (75)		0.95 (20) 1.24 (26)		1.06 (35)	1.29 (40)

Note: Juveniles and infants are considered immature individuals.

Abbreviation: OMU, one-male unit.

TABLE 6 Estimation of proboscis monkey population size in Balikpapan Bay over a 10-year scenario, based on Hutan Kariangau as a reference subpopulation

Year	Habitat size in Hutan Kariangau (km^2)	Hutan Kariangau (group/km^2)	No. of groups in Hutan and Teluk Kariangau	Habitat size outside censused area (km^2)	Estimated number of groups (+censused groups)	Average group size Hutan Kariangau (individuals/group)	Estimated number of individuals
2007	14.29	1.19	51	185.95	221 (272)	9.56	2603
2012	13.94	1.00	54	181.29	181 (235)	9.20	2165
2017	13.16	1.14	60	176.65	201 (261)	6.89	1801

Note: Population values from 2012 are taken from Scott (2012). Data of proboscis monkey habitat outside censused area of Balikpapan Bay are based on Toulec (2018).

habitat loss in Balikpapan Bay to be 0.78%, which is unlikely to reflect a dramatic population decline of 3.93% per year extrapolated from Figure 2 in Stark et al. (2012) in a 10-year period.

The main factor responsible for the predicted population decline of proboscis monkeys using the PVA model were forest fires that have already caused extensive loss of forests and wildlife habitats in Southeast Asia (Fuller et al., 2004). While fires do not directly burn the mangrove forest in Balikpapan Bay, 27% of the proboscis monkey habitat in Balikpapan Bay is burnable terrestrial forest, which may provide the proboscis monkeys with some of the important food resources (Koubek et al., 2018, unpubl. data). Therefore, the finding that the population in Balikpapan Bay did not decline cannot be explained by the absence of forest fires. During the 2015 ENSO event, extensive forest fires arose around Balikpapan Bay (Pro Natura Foundation, 2016), yet it only affected proboscis monkey habitats on a small scale (Toulec et al., 2020). The forests burned mainly along the ridges and on the slopes of hills, while the proboscis monkey habitats located along rivers and coast probably remained relatively humid and more resistant to the fire during this ENSO event.

Nonetheless, most of the coastal forest in Balikpapan Bay has already suffered from burning at various points in the past, frequently because of human encroachment, land speculations, or small-scale agriculture. The continuous presence of proboscis monkeys in these degraded forests proves that even burned forests can provide sufficient food resources for this species if the tree cover is not removed completely and permanently. All other colobines that share the same habitat with the proboscis monkeys in Balikpapan Bay have already almost disappeared from the coastal forests. In 2021, we observed the last 1–2 groups of the silvered langurs *Trachypithecus cristatus* sharing the habitat with proboscis monkeys, each in a different river system. This species has recently disappeared from at least two other river systems, where it has been observed by Stanislav Lhota or by local informants. Maroon langurs *Presbytis rubicunda* and white-fronted langurs *Presbytis frontata* have been heard by Stanislav Lhota from the coastal forest in the past decade but now they are confined to forest several hundred meters from the coast, no longer overlapping with the distribution of the proboscis monkeys. These findings highlight the importance of protecting the degraded secondary coastal forests as an important habitat for these endangered species.

Proboscis monkey groups were encountered in each river system of the Balikpapan City administrative area. The number of groups on individual rivers fluctuated greatly during consecutive censuses, contrary to the relatively stable total group counts observed for the whole population. This suggests that the groups continue to freely range across neighboring river systems. Furthermore, an increased ratio of females to males (Table 5) could indicate a male-biased emigration to surrounding areas. Notable exceptions include a 4.2 km broad gap of the Kariangau Industrial Area, which currently acts as a barrier separating two major subpopulations within the Balikpapan City administrative area of Balikpapan Bay, and a similar but much narrower barrier of industrialization/urbanization between rivers Wain and Somber.

The Teluk Kariangau subpopulation, notably those groups that range along the Somber River, show several oddities in population size, structure, and dynamics that may be related to the process of advancing fragmentation. The OMUs on the Somber River were on average larger than proboscis monkey groups observed elsewhere in Balikpapan Bay (Pemaluan River, Riko Mati River, and Hutan Kariangau; Table 4) as well as those observed by Bennett and Sebastian (1988) in Samunsam, or Matsuda et al. (2020) on Kinabatangan River in Sabah. Boonratana (1993) and Murai (2004) detected OMUs of similar size on the Menanggul River, a Kinabatangan River tributary, however this area represents a freshwater riparian forest, very different in vegetation and nutrient diversity from the Somber River mangrove forest. Furthermore, the population density on the Somber River was unusually high, compared to other localities (Table 1), even if we keep in mind the methodological differences among various studies. Only Yeager (1989) recorded unusually high population density in Tanjung Puting National Park, which again represents a freshwater riparian forest. Finally, Somber is the only river within the study area with a consistently increasing population size (Figure 2), and a high ratio of immatures to adult females (Table 5). This suggests that the population is increasing.

The unexpected finding of increasing population sizes may, however, suggest a delay before the proboscis monkey population growth reverses in response to depletion of food resources in the shrinking habitat. The increased mortality of *Sonneratia alba* (Lythraceae) trees, the major food resource of proboscis monkeys in the Somber River, may be a direct consequence of the increasing population of the monkeys, and its decline may be detrimental to the future population changes (Toulec et al., 2020). The current situation in Somber River appears to mirror an initial stage of the previously

described collapse of a proboscis monkey population in Pulau Kaget Nature Reserve (Meijaard & Nijman, 2000b).

In Hutan Kariangau, the average sizes of both types of groups decreased, most likely because of the localized habitat loss and degradation primarily due to the ongoing industrial development (Toulec et al., 2020). There was the relative stability of the population size in terms of group counts, but smaller average group sizes were also observed in degraded sites of Sabah (Matsuda et al., 2020). The whole Balikpapan Bay population estimate, based on extrapolation of Hutan Kariangau as a reference subpopulation, would suggest a radical decline of the population (Table 6), which would be solely due to the smaller estimated group size, while the number of groups follows a different pattern (Figure 2). However, opportunistic data collected in 2012 in another part of Balikpapan Bay (outside Balikpapan Bay area) do not suggest that the decline of group size occurs in the whole area.

Following approval of a new spatial plan for the Balikpapan City administrative area, almost all non-mangrove proboscis monkey forest habitat has been allocated for industrial development (Peraturan Daerah Kota Balikpapan No. 12/2012 Tentang Rencana Tata Ruang Wilayah Kota Balikpapan Tahun 2012–2032). This proposed deforestation will inevitably lead to the isolation of most of the river systems within the Balikpapan City administrative area and will accelerate the rate of habitat loss, which may, in turn, fulfill Stark et al.'s (2012) predictions of rapid population decline.

4.1 | Group types, age, and sex composition

There was an inconsistent pattern of the number of AMUs in the population, with very low values obtained in 2012 (Figure 2). One possible explanation would be migration between the Balikpapan Bay administrative area (namely, Hutan Kariangau) and the neighboring PPU Regency administrative area in the north, which has not been censused yet where the habitat and population remain continuous. Alternatively, there may be a pattern of subgrouping (splitting and rejoining) of the larger AMU, which may partly obscure the results. Subgrouping on an almost daily basis as described by Bennett and Sebastian (1988). One of the authors (Stanislav Lhota) observed similar behavior in 2020 on Riko Mati River in a large AMU of 16 individuals.

However, the most plausible explanation seems to be the misclassification of some groups. AMUs of proboscis monkeys are relatively small and silent, and they sometimes choose their sleeping sites in close proximity to OMU (Salter et al., 1985; Yeager, 1991). As a result, the observers may fail to classify them as a distinct group. Some AMUs contain small juveniles and may therefore resemble OMUs. Boonratana (2002) described several cases of females associated with AMU for a few consecutive days, which could also lead to a group misclassification. Stanislav Lhota has also noticed an adult female in an AMU in Hutan Kariangau in 2007 and in several AMUs in the Riko watershed in 2020 (Darman & Lhota, pers. comm., February 12, 2021). In addition, subadult males may be confused with adult females if viewed briefly and from a distance. All these factors may lead to the misclassification of AMUs as OMUs.

On the other hand, OMUs may be confused with AMUs, too, when they are small, are silent and forage or rest some distance from the riverbank, causing females to be invisible to observers. We, therefore, suggest that the data on the proportion of the two types of groups, collected during relatively fast observations need to be treated with caution. Still, we highly recommend distinguishing between the two types of groups during censuses or surveys. Although the similar-sized AMU and OMU may be misidentified, the overall difference between the average group size of these two group types is rather large (Tables 3 and 4), and the proportion of the two types of groups varies for different river systems. The consequences of misclassification of similar-sized groups would be less serious compared to lumping AMUs and OMUs together and using the overall average group size to estimate the total population.

We did not encounter any multimale–multifemale reproductive groups during our censuses, thus confirming the strictly one-male pattern of the proboscis monkey reproductive units. Occasionally, an additional subadult male was detected in OMUs during our three censuses (both Teluk and Hutan Kariangau) and on two more occasions in the Pemaluan and Riko (additional adult male) watershed outside the study area (Darman & Lhota, Personal communication, February 12, 2021). This corresponds with other studies that found only a few subadult males within an OMU (Bennett & Sebastian, 1988; Matsuda et al., 2020) or even none (Yeager, 1990a). The very low occurrence of subadult males in OMUs contrasts with a high proportion of juveniles in OMUs, which included numerous males (although we were not able to quantify the exact proportion of juvenile males). This suggests that the juvenile males would leave OMU before they turn into subadults. The dispersal of males has been previously described as common (Bennett & Sebastian, 1988).

There may be one or more adult males in each AMU. The number of adult males in AMU appears to be related to the number of OMUs in the same subpopulation. This may explain the decrease in the proportion of the adult males present in AMUs in the Teluk Kariangau subpopulation over the decade of observation (0.58 in 2007 to 0.14 in 2017; Table 5). The increased number of OMUs (24 in 2007 to 34 in 2017; Table 2) probably represents more opportunities for adult males to acquire and/or maintain the position of the breeding male in an OMU, rather than joining an AMU.

The most numerous age and sex classes in OMUs were the adult females. The number of adult females per adult male showed opposite trends in the two subpopulations from 2007 to 2017. We observed a steep increase in the proportion of adult females in Teluk Kariangau (namely, the Somber River) and a slower decrease in Hutan Kariangau (Table 5). This highlights the importance of monitoring the population dynamics on a subpopulation level.

Both subpopulations showed an increased number of immatures (juveniles and infants) in 2017 (Table 5). According to Boonratana (2011), high numbers of infants could correlate with adult females' time spent feeding. This is supposed to coincide with higher rainfall, when young leaf and young fruit production increases. In Balikpapan

Bay, there is a secondary rainfall peak from March until May, which corresponded with the census period in 2017. Moreover, studies by Yeager (1990b) and Boonratana (2011) detected the highest occurrence of mating in August and September. This would situate the subsequent births between February and March, which could also explain increased observation of immatures in 2017.

Seasonality in reproduction in proboscis monkeys remains poorly understood and birth peaks often vary in different locations. This could even change in different years in the same location (Boonratana, 2011; Murai, 2006). Therefore, we recommend taking seasonality into account in planning population surveys and monitoring. We recommend conducting the fieldwork before the rainy season, which would combine the advantage of not losing time in the field due to rainy weather, and has the advantage of not having the group size counts inflated due to the birth peak.

The two different methods used in this study (opportunistic group counts in 2007, and systematic group counts in 2017), lead to different results. The maximum size of recorded groups during the opportunistic group counts was generally smaller and never included a group with more than 17 individuals (Table 3, Table S3). We believe that the rate of successful counting during the opportunistic group counts decreases with group size. Large groups are often only partially counted and, consequently, were not included in group size calculations. An alternative approach to attempt to count every group encountered would inevitably lead to incomplete counts. We would, therefore, recommend using repeated systematic group counts of all groups in selected rivers instead of one-time, opportunistic group counts. Systematic group counts should be conducted as a supplementary study to the census on the group level. It is time-consuming (we spent nearly the same amount of time on systematic group counts in selected rivers as we spent counting groups in the whole area), but we believe that the increased reliability of data is worth this additional effort. In our study, due to the limitations of the opportunistic group counts in 2007, we can currently assess the population change in Balikpapan Bay only at the level of a number of groups, although not the number of individuals.

4.2 | Estimating total population size

The population of Balikpapan Bay was initially described by Meijaard and Nijman (2000a) to contain 100–1000 proboscis monkeys. Manansang et al. (2004), in their PHV analysis, included only populations that they "felt might be viable in the long-term (populations of ≥100 individuals)" (p. 7). Their exclusion of Balikpapan Bay suggests they assessed it to contain fewer than 100 individuals. After the first population census (2007 by Stanislav Lhota), Stark et al. (2012) used an estimate of 1400 individuals. Our latest findings, based on the Hutan Kariangau serving as a reference subpopulation for the rest of the habitat, reveal a conservative estimate of the even larger population, comprising of some 1800 individuals. The currently ongoing census in the PPU Regency administrative area (Darman et al., 2020, unpubl.) shows that even this estimate most likely underestimates the total size of the Balikpapan Bay proboscis monkey population.

Boonratana (1993) surveyed the Lower Kinabatangan in 1991 and 1992 and observed 832 proboscis monkeys. He suggested the total number could be at least twice that if he had included areas that were not surveyed. Sha et al. (2008) included those previously unsurveyed areas by Boonratana (1993) and estimated the population at 1340 individuals; whereas Matsuda et al. (2020), estimated it to be 1960 individuals. These differences in estimates, as seen in the Lower Kinabatangan and Balikpapan Bay, most likely reflect different sampling efforts, area coverage, and an increased understanding of the biology of the species rather than substantial changes in numbers. Naturally, differences in forest structure and habitat availability may also be identified as influencing factors.

While our current method appears to be robust enough to monitor the long-term changes of a subpopulation within a specified area, the data cannot be easily applied to estimate the total population size for a more extensive area, such as the whole of Balikpapan Bay. First, even a small error or random nonsignificant fluctuation in the reference subpopulation size estimate would be inflated when referring to an extensive area. This would be further magnified for estimates in the number of individuals rather than at the group level. For instance, if we expanded our 2012 reference dataset with data collected on two river systems outside Balikpapan City administrative area ($n = 3$ groups, Scott, 2012) the average group size would decrease from 9.20 to 7.35 individuals/km^2; giving us a population estimate of 1800 individuals instead of 2165, thus altering the population trend. Second, the reference area may not be truly representative of the whole area. Balikpapan Bay is not a homogenous habitat. Different parts of the bay are specific in terms of forest type composition, environmental pressure, habitat degradation, and the level of human disturbance. Therefore, it is difficult to choose a subpopulation, which would represent the remaining parts of Balikpapan Bay. As an extreme example, if we adopted Teluk Kariangau (instead of Hutan Kariangau) as our reference subpopulation, the results will show a population increase in the whole Balikpapan Bay from 1705 individuals in 2007 to 4182 individuals in 2017. Without any doubt, this would be an erroneous result, as the high population density observed in the Somber River most likely represents an unstable increase in this population fragment.

To overcome these limitations, we suggest that the proboscis monkey populations of high conservation concern, such as in Balikpapan Bay, should have a complete census. This would eliminate the error caused by extrapolating the density of selected reference subpopulations to obtain the total population size. Given the above-described sources of error, we consider the number of groups observed, rather than the estimated number of individuals, as the best currently available measure of the Balikpapan Bay population status and dynamics. However, this means that the changes in population size due to changing group size would be missed. While there is no doubt that the number of individuals describes the population better, we would need to fully count a much larger proportion of groups to

obtain good estimates of the average group size that could be used to extrapolate to the whole population.

Censusing the whole population at the group level with a high proportion of fully counted groups would be time consuming and expensive, yet we believe that for the purpose of long-term monitoring of a large population it only needs to be done as an initial step to properly understand the total size and structure of a given population. For the purpose of further long-term monitoring of population changes and alerting the relevant organizations and institutions of any worrying trends, the method of censusing selected representative subpopulations in 5-years intervals, coupled with the remote-sensing monitoring of the habitat change (Toulec et al., 2020) might prove to be a reasonable compromise between costs and accuracy of the monitoring program.

The finding, that the major proboscis monkey populations that have been subject to the long-term monitoring programs (Klias Peninsula, Bernard et al., 2021; Lower Kinabatangan, Matsuda et al., 2020; Balikpapan Bay, this study) remain relatively stable, does not mean that the population of the species as a whole is not declining. The intensive monitoring effort is always likely to be connected to the intensive conservation effort, which may be crucial for ensuring the stability of the population. To assess the status of the whole species, we also need to look at the rate of habitat decline and other changes in populations that are not subject to conservation intervention.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

AUTHOR CONTRIBUTIONS

Tadeáš Toulec: Data curation (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); software (equal); supervision (equal); validation (equal); visualization (equal); writing – original draft (equal); and writing – review and editing (equal). **Stanislav Lhota**: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); validation (equal); writing – original draft (equal); and writing – review and editing (equal). **Katherine Scott**: Data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); resources (equal); validation (equal); writing – original draft (equal); and writing – review and editing (equal). **Wawan Kustiawan**: Formal analysis (equal); project administration (equal); writing – original draft (equal); and writing – review and editing (equal). **Vincent Nijman**: Conceptualization (equal); formal analysis (equal); funding acquisition (equal); project administration (equal); supervision (equal); writing – original draft (equal); and writing – review and editing (equal).

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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