DOI: 10.1111/1440-1703.12373



Effects of anthropogenic disturbance on group densities of Thomas' langurs (*Presbytis thomasi*) within a lowland tropical forest, north Sumatra

Emma Hankinson^{1,2} | Amanda H. Korstjens² | Ross A. Hill² | Serge A. Wich³ | Helen D. Slater^{1,4} | Abdullah Abdullah⁵ | Supradi Supradi⁵ | Christopher D. Marsh^{1,6} | Vincent Nijman¹

¹School of Social Sciences, Oxford Brookes University, Headington Campus, Oxford, UK

²Department of Life and Environmental Sciences, Bournemouth University, Christchurch House, Talbot Campus, Poole, UK

³School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK

⁴School of Natural and Environmental Sciences, Newcastle University, Newcastle Upon Tyne, UK

⁵Fakultas Biologi, Universitas Syiah Kuala, Darussalam, Banda Aceh, Indonesia

⁶Department of Biology, University of New Mexico, Albuquerque, New Mexico, USA

Correspondence

Emma Hankinson, School of Social Sciences, Oxford Brookes University, Headington Campus, OX3 0BP Oxford, UK. Email: besehank@hotmail.com and 19039459@brookes.ac.uk

Funding information

Bournemouth University; International Primatological Society; Sumatran Orangutan Conservation Programme

Abstract

Ecosystems around the globe are facing irreversible impacts due to climate change, habitat destruction, hunting, and an ever-increasing human population. Estimating densities of species across their geographical range helps us to understand natural variation and anthropogenic effects on species densities and to assess the effectiveness of existing conservation measures. Various methods have been used to produce accurate and precise population density estimates, each with associated limitations. Acoustic surveys for species producing loud calls have become common due to their ease of use, low cost, and reduced timescale. Relative to many other mammal taxa, primate species have been studied extensively, producing a wealth of data on socioecology and behavior, but for most species, density estimates over large geographical ranges are still lacking. We used an acoustic spatial capture-recapture model to estimate group density of unhabituated Thomas' langurs (Presbytis thomasi), a primate endemic to the Indonesian island of Sumatra, over a 60 km² area of lowland dipterocarp forest. We then assessed if vegetation structure and distance from human habitation affected density estimates. Estimates of group density differed almost threefold between survey locations (from 2.79 to 8.08 groups/km²); there was no clear relationship with forest structure, but there was a significantly positive relationship between group density and distance from human habitation, with an increase of 0.38 groups/km² for every km of distance. Although large-scale logging within the Sikundur region ceased ~30 years ago, the impacts of logging continue to have detrimental effects on the species within the area.

KEYWORDS

acoustic surveys, anthropogenic disturbance, leaf monkeys, primates, Thomas' langur

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. Ecological Research published by John Wiley & Sons Australia, Ltd on behalf of The Ecological Society of Japan.

1 | INTRODUCTION

Due to human impacts, we are currently facing what some scientists are calling "the sixth mass extinction crisis" (Barnosky et al., 2011). Species are disappearing almost 100 times faster than the rates that have occurred over the last tens of millions of years (Ceballos et al., 2015). Human population growth, industrialization, and environmental transformation (e.g., induced climate change, habitat destruction and degradation, hunting, and disease) have led to ~38% of floral and faunal species now being threatened with extinction (IUCN, 2020). Conservation interventions and wildlife management are increasingly important globally in an attempt to safeguard remaining habitats and species (Lambert & McDonald, 2014). To aid successful management plans and guide conservation actions, it is essential to know the population density of animals throughout their range and to determine the environmental factors that affect these densities (Dacier et al., 2011; IUCN, 2020; Marques et al., 2013).

Population abundance and density estimates of species often form the baseline data for studies investigating ecological and social limitations to populations, reductions in species abundance over time, species flexibility to habitat change, and impacts of diseases on populations (Gibbons et al., 2000; Plumptre et al., 2013; Voigt et al., 2018). Furthermore, the effectiveness of existing conservation measures ultimately relies on these population estimates to monitor impacts (Measey et al., 2017; Phoonjampa et al., 2011; Plumptre et al., 2013). However, many species are difficult to locate and observe, and therefore obtaining reliable and accurate information on density and abundance is problematic (Costa et al., 2020; Lambert & McDonald, 2014; Roffler et al., 2019), especially in tropical forest ecosystems.

Asia's tropical forests are being lost and are undergoing rapid anthropogenic degradation and fragmentation at unsustainable rates of ~0.9% each year (Turubanova et al., 2018). Many species occupying these habitats are declining due to various factors, such as alterations in resource availability, increased resource (e.g., food and space) competition within and between species, edge effects causing changes in local climatic conditions, increased hunting and an increased risk from disease and parasitic infections (Bolt et al., 2019; Chapman et al., 2004; Klaus et al., 2018; Nijman, 2010; Reed & Bidner, 2004; Sterck, 1999). However, access to many remote tropical forest areas to establish species monitoring programs is logistically challenging. Dense tropical rainforest habitats limit visibility of many animal species, especially in regard to arboreal species that are positioned high within the canopy (Alempijevic et al., 2022; Dacier

et al., 2011; Neilson et al., 2013). Shy, elusive, or cryptic species are also difficult to locate visually and often flee or hide when human observers approach. Therefore, densities of these elusive species can be underestimated if based on visual survey methods (Campbell et al., 2016; Dacier et al., 2011). Moreover, actual data collection for such studies can be extremely challenging, both logistically and financially, often requiring suitably trained, experienced researchers to habituate groups prior to survey, and to undertake surveys for a significant amount of time (often >6 months) to obtain accurate and precise population estimates (Lambert & McDonald, 2014). Other issues to be resolved postsurvey include the quality of data obtained and the methods to use for analysis.

Many tropical primate species have been studied extensively; however, many of these studies have concentrated on a single location or a single population for many years, most likely due to the time spent habituating groups and individuals (Ashbury et al., 2020; Cheyne et al., 2019; Lonsdorf et al., 2020; Wich et al., 2007). Although these studies have been extremely important in regard to species ecology and behavior, data are still lacking on either their presence/absence in areas across their range or their population status within these areas. This is generally due to the difficulty in surveying unhabituated individuals living in these challenging tropical forest landscapes.

For species producing loud, territorial calls, acoustic monitoring surveys are becoming increasingly common. These surveys do not require groups to be habituated prior to the start of the study due to the nonreliance of visual sightings and as such, can be used for both diurnal and nocturnal species (Efford et al., 2009; Marques et al., 2013; Stevenson et al., 2020). Furthermore, calls can be detected over much greater distances in comparison to visual sightings, enabling species to be surveyed over a larger geographical range. Acoustic techniques now more commonly incorporate spatial capturerecapture (SCR) models to estimate population density from acoustic detections and subsequent redetections of individuals and/or groups across space (auditory posts), rather than across time (Stevenson et al., 2020). Acoustic techniques have been used to estimate population data for a variety of taxa and species, including cetaceans (Harris et al., 2018; Klinck et al., 2012), birds (Buxton et al., 2013; Lambert & McDonald, 2014; Sebastián-González et al., 2018), amphibians (Measey et al., 2017), terrestrial mammals (Wrege et al., 2017), and arboreal primates (Dacier et al., 2011; Hankinson et al., 2021; Kidney et al., 2016).

The Thomas' langur (*Presbytis thomasi*), a primate species endemic to the Indonesian island of Sumatra, has been studied extensively (Gurmaya, 1986; Manullang, 1999; Rijksen, 1978; Steenbeek, 1999; Sterck, 1996; Sterck et al., 2005; Syaukani, 2012; Ungar, 1994, 1995, 1996; Van Schaik et al., 1983; Wich et al., 2003, 2004, 2007; Wich & De Vries, 2006; Wich & Sterck, 2003; Wilson & Wilson, 1976). As in other primate species, most of these studies were undertaken at a small number of locations across their range. Despite the extensive knowledge obtained on Thomas' langur socioecology and behavior from these studies, we have surprisingly little data on their occurrence and density, and how this is related to environmental characteristics and human disturbance at a landscape scale. Here, we aim to fill this gap by reporting on a study undertaken in a ~60 km² area of lowland forest near Sikundur, located on the eastern edge of the Gunung Leuser National Park (GLNP). Specifically, we aim to: (a) estimate group densities over a large geographic area using active acoustic monitoring and an acoustic SCR (ASCR) model and (b) relate group densities to vegetation characteristics and distance to human habitation.

Based on previous studies (Gurmaya, 1986, 1989; Nijman, 2021; Rijksen, 1978), Thomas' langurs show a level of flexibility in their response to canopy structural changes by their increased use of terrestrial locomotion. Therefore, we predict that there will be no significant differences in group densities between areas showing varying levels of structural disturbance to the canopy (tree connectivity, tree crown area, tree height, etc.). Studies have shown that anthropogenic disturbance negatively affects densities and group composition of various langur species (Nijman, 2010, 2021; Sterck, 1999); therefore, we predict that group densities will decrease when they are located closer to human settlements.

2 | METHODS

2.1 | Ethical statement

The study was completely observational and involved no interference with any primate groups, thus no reviews requiring ethics committees were required. All field research was permitted by the Ministry of Research, Technology and Higher Education of the Republic of Indonesia (RISTEKDIKTI), and Gunung Leuser National Park authorities (TNGL). This study adhered to all the legal requirements of Indonesia, with the required research visa acquired (Permit No. 50/SIP/FRP/E5/Dit.KI/II/2016) and a SIMAKSI issued from the National Park authorities prior to study.

2.2 | Survey area

The study area (centered at 04°58'-04°59"N and 98°04′-98°05″E) is situated partly in the Sikundur forest, located on the eastern border of the GLNP (7927 km²), north Sumatra, Indonesia. This national park is one of the largest intact stretches of rainforest remaining in Southeast Asia, and is a UNESCO World Heritage site (Figure 1). The survey area is composed of lowland dipterocarp forest mixed with alluvial forest along the banks of the Besitang river (Knop, 2004). The forest elevation ranges from 30 to 100 m A.S.L., with a monthly temperature of 27.4°C (Roth mean et al., 2020) and a humid climate producing 2000 to 3000 mm of rainfall annually. The Sikundur area was selectively logged intermittently between the 1960s and 1990s, causing severe damage to large areas of forest including the removal of large trees, creation of logging roads and the formation of large canopy gaps. Although over the last 30 years, natural regeneration has occurred in parts (Basyuni et al., 2019; Priatna et al., 2004), even with the full protection of a national park status, illegal logging, bird trapping, and hunting still occur.

COLOGICAL WILEY 3

2.3 | Study species

The Thomas' langur or north Sumatran leaf monkey is a colobine species endemic to the northern part of the Indonesian island of Sumatra, mainly distributed north of the Simpangkiri and Wampu rivers (Wilson & Wilson, 1976). The species is listed as Vulnerable on the IUCN Red List, with an estimated population decline of >30% over the last 40 years, primarily due to loss of habitat (Setiawan & Traeholt, 2020).

Thirteen different vocalizations produced by Thomas' langurs have been recognized and described by Gurmaya (1986). The most notable is the loud, long-distance call emitted by each group's alpha male, performed in the early morning from their sleeping tree and can be heard up to 1 km (Wich & Sterck, 2010). Its primary function is territorial defense in between-group encounters; a call from one male generally elicits a loud call response from the males of neighboring groups. The Thomas' langurs inhabiting the Sikundur forest are unhabituated, and although studies in regard to male loud calls have been undertaken on groups located near the research station (Wich et al., 2008), accurate and precise group density estimates within the area were unknown prior to this study.

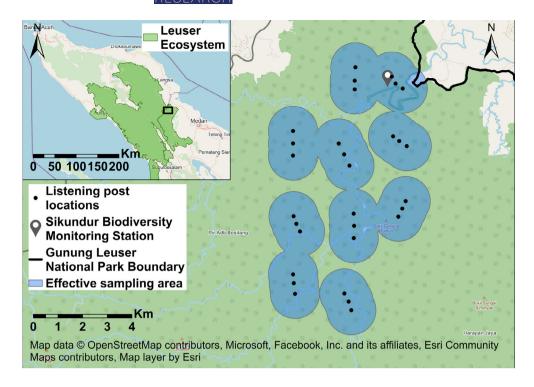


FIGURE 1 Location of the total survey area in north Sumatra, showing 10 survey locations each with 3 listening posts used for active acoustic monitoring of Thomas' langur groups, March–August, 2016, north Sumatra. [Color figure can be viewed at wileyonlinelibrary.com]

2.4 | Data collection

^₄ WILEY_

ECOLOGICAL

We estimated the group density of Thomas' langurs between March 10, 2016 and August 1, 2016 using active acoustic monitoring. We established 10 survey locations over an approximately 60 km² area of lowland dipterocarp forest within GLNP and positioned our first survey location within the Sikundur research area, on the eastern edge of the park's boundary (Figure 1). We placed subsequent survey locations to the west and south of our initial location as human habitation (villages, roads, farms) were present to the north and east, outside of the national park boundary. Survey locations represented a range of habitat types and structural variation created from the areas historical logging practices.

Within each survey location, three auditory sampling posts were placed linearly and spaced between 300 and 500 m apart. Spacing variation was determined by topography or thick vegetation, which may restrict where calls could be detected or where the direction of the call might be misinterpreted. Thomas langur calls can travel and remain detectable up to a maximum hearing range of 1 km, and the diameter of a Thomas langur home range is ~500 m, based on an average home range size of 35 ha (Gurmaya, 1986; Steenbeek & van Schaik, 2001; Sterck, 1996). Therefore, the post spacing meant calls from each separate group could be detected from more than one auditory post in each survey location, which allowed groups to be mapped each day. The effective sampling area of each location was calculated in QGIS (v. 2.18.18) using a buffer of 1 km around each listening post and omitting areas of overlap (Table 1). As the langur groups within the area were unhabituated, we used this measurement based on calling detection distances from other primate vocalization studies in rainforest environments, such as gibbons (Hamard et al., 2010; Hankinson et al., 2021; Lee et al., 2015). As our furthest estimated distance to a call within this study was 900 m, we believe no call produced <1 km away from a post would be missed. We ensured that each auditory post in each survey location was at least 2 km apart from auditory posts in neighboring survey locations, to ensure there was no double counting of calling groups detected from these adjacent locations.

We surveyed each location for four consecutive days with at least one observer present at each auditory post. Rain is known to negatively affect vocalizations in primates (Batist et al., 2022; Lee et al., 2015) and therefore no surveys were conducted on rainy mornings. Each surveyor arrived at their post at 04:30 h and stayed until 07:00 h, remaining still and quiet throughout. Arrival was prior to sunrise, which prevented disturbing the langur groups before they awoke. When a Thomas' langur call was heard, the observer would record the time, compass bearing and estimated distance to the call. Calls are unique to this species, highly recognizable in the field and easily distinguished from other primate species present. We used only the first detected vocalizations (known as pre-dawn loud calls, often persleeping and highly formed from their tree

TABLE 1	Thomas' langur group density estimated using
acoustic spati	al capture–recapture (ASCR) methods and survey
location area	in north Sumatra, March–August 2016.

Survey location	Survey location area (km ²)	Groups heard (<i>N</i>)	Estimated density (groups/km ²)	2.5% CI-97.5% CI
1	3.54	7	3.88	2.70-4.09
2	4.91	6	2.79	2.18-3.36
3	4.50	7	3.76	2.58-4.92
4	4.53	9	3.64	2.78-4.47
5	5.12	6	5.12	2.33-4.37
6	5.12	8	3.01	2.13-3.89
7	5.12	8	3.04	2.63-6.98
8	4.61	9	5.45	3.88-7.63
9	4.72	10	5.65	3.66-7.65
10	4.48	13	8.08	6.37-9.82

distinguishable from other langur vocalizations) made by the male within each group from each auditory post for the analysis and discarded any subsequent calls detected later (either repeated loud calls or other langur vocalizations). Thomas' langurs are extremely agile, move frequently between these morning territorial calling bouts and are often stimulated to call by adjacent calling groups (Assink et al., 1999). As the population within the area was unhabituated, and the calls were generally made prior to sunrise in low light, it would be impossible to assess whether the later secondary calls were made by the same groups identified in producing the first detected calls, thus adding these to the analysis may skew the density estimation.

Each day the number of groups detected within the survey location was ascertained by mapping the location of the calls using the bearing, distance and matching time stamps from all auditory posts. Field teams consisted of at least three observers (one at each listening post), and the same observers conducted the acoustic surveys in all 10 locations. All observers were experienced in fieldwork with primates in Indonesian rainforests. We trained these individuals for 1 week prior to data collection to ensure methods were understood and data collection was consistent. Training consisted of Thomas' langur call identification, compass use, estimating distances within different rainforest terrains, and both group and individual practice dawn recordings. Error in distance estimates was expected and was not detrimental, as this measurement only aided group mapping and was not a requirement of the subsequent analysis, and therefore any error would not affect density estimates.

COLOGICAL WILEY 5

2.5 | Analysis of acoustic data

We produced a group density estimate per survey location for Thomas' langurs by analyzing the vocal data using an ASCR model developed by Stevenson et al. (2015). The ASCR model is recommended by the IUCN Species Survival Commission (SSC) Primate Specialist Group Section on Small Apes as an accurate way of analyzing primate acoustic data (Cheyne, unpubl. data; Stevenson et al., 2015) and has recently been used to accurately estimate the group density of Sumatran gibbons (Hankinson et al., 2021). The data were analyzed using an online interface developed by Charlotte M. Jones-Todd (Jones-Todd, 2019; Stevenson et al., 2015). This interface works in conjunction with the ASCR package in R, which provides software and implements the fitting of the SCR model for acoustic data. The model incorporates bearings and distances to each call to provide additional information about call locations, but integrates measurement error in these variables. Therefore, unlike other non-SCR analysis methods such as distance sampling, that require very accurate bearing and distance estimates, high accuracy in bearing and distance measurements is not a requirement, and can be used even if they are subject to considerable measurement error (Borchers et al., 2015).

The "recapture" data from acoustic surveys are detected virtually from multiple posts by more than one observer, therefore these recaptures are redetections, occurring at different points in space, rather than time (Stevenson et al., 2020). Thus, capture histories indicate which post detected each call. We input the group ID, occasion (day), post ID, survey location ID, bearing, and estimated distance of each identified group for all survey locations into the interface/model and applied a half normal detection. This assumes the probability of detection has a half normal function of distance, with the probability of detection (g0) at distance zero fixed at 1, and decreases as distance from each auditory post increases. We expected that we would not miss a group at 0 m from each post as observers arrived at each post ~2 h prior to sunrise and remained still and quiet. We often recorded calls from directly above us or close to our post location, demonstrating our arrival or presence did not disturb the groups from their sleeping trees.

However, the density parameter produced by ASCR from the above data is the call density (calls per hectare accumulated across the whole survey period), as the data provided to the model are capture histories for each call (Stevenson et al., 2015). As we surveyed each location for 4 days, we divided this value by 4, which provides a daily calling group density estimate for each survey location. To convert this value to a group density estimate, we

6 WILEY- RESEARCH

required a daily calling probability for langurs. The calling probability (p1); the probability of a call happening on any 1 day at any survey location was calculated from our data using the following equation (Vu & Rawson, 2011):

$$p(1) = \frac{1}{2} \left(3 \frac{\sqrt{4.N}}{n} - 3 \right),$$

where n = mean number of langur groups detected each day and N = cumulative number of langur groups detected over the entire survey period of 40 days. Vu et al. (2018) have suggested for gibbons, calling probability estimates can be negatively biased if calls beyond a maximum distance of ~700 m are used in this calculation, as it voids the assumption of a closed population. Therefore, any calls with an estimation >700 m were omitted from this calculation to prevent overestimation of group density. This provides us with our group density estimate per survey location. As the model provides the data in density/ha, we converted these into groups/km² by dividing by 100.

2.6 | Measurements of vegetation structure and distance from human habitation

A vegetation structure analysis of the 10 survey locations was completed as part of a study running concurrently on gibbon population density within the same location (Hankinson et al., 2021). This research revealed a relationship between gibbon density and forest structure and therefore, we also used the vegetation data in this study to determine if there was a relationship between vegetation structure and Thomas' langur densities. At each survey location, between four and six $25 \text{ m} \times 25 \text{ m}$ plots were randomly placed (using the "create random points" function in ArcMap (version 10.4)) in which the following parameters were recorded for every tree with a diameter at breast height (DBH) ≥ 10 cm: (i) DBH (cm); (ii) tree height (m); (iii) height to first major bole (m); (iv) crown area (m^2) ; and (v) tree canopy connectivity (%), determined visually by the percentage of the tree crown connected to the neighboring tree crown. For each tree measured, the DBH was used to calculate the basal area (m²). Vegetation data were then summarized for each array location. Mean bole height (m), mean crown area (m²), and mean crown connectivity (%) were calculated for each location. Lorey's mean height (i.e., the mean tree height weighted by the basal area) was calculated for each location using the "lorey.height" function

from the R package "sitreeE" (Antón Fernández, 2019). In addition, the distance of each survey location to the forest edge (defined as the nearest area where natural forest cover is no longer present) was measured from imagery available in Google Maps (in the same year as the study was undertaken). This was used to determine if human disturbance affected the density of Thomas' langurs within the survey locations. This distance is defined as the distance to "human habitation" hereafter.

2.7 Statistical analysis

We used a generalized linear model (GLM) to determine the effects of Lorey's mean height, mean bole height, mean crown area, mean connectivity, and distance from human habitation on Thomas' langur group density. The GLM was fitted with a Gaussian distribution using the "glm()" function in R version 4.0.0. We used the vif() function from the "car" package (Fox et al., 2012) to calculate the variance inflation factor and check for the effects of collinearity among the predictor variables. Any variables with a VIF of higher than five were removed from the model. We then used the "dredge" function from the "MuMIn" package (Barton, 2020) to determine which combination of variables produced the best model performance based on their AIC criterion. The full reproducible code is available in Data S1.

3 | RESULTS

3.1 | ASCR group density analysis

The calculated calling probability was p(1) = 0.9961 for Thomas' langur calls over the 40-day survey period across all 10 survey locations. The estimated detection function of the model showed detection probability severely declined at a distance of 1 km (Figure 2), supporting our estimated effective listening distance of 1 km.

We recorded a total of 328 calls equating to 83 different groups of Thomas' langurs across the 10 survey locations. Thomas' langurs were present in all 10 locations surveyed, and estimated group densities were between 2.79 and 8.08 groups/ km^2 (Table 1).

3.2 | Vegetation structure and distance from human habitation

A summary of vegetation structure variables for each array location is given in Table 2. Bole height had a variance inflation factor of 5.37 and was therefore removed from the model. All other predictor variables had a variance inflation factor below five. The best model fit was obtained using only distance to human habitation as a predictor variable (AIC = 36.30, compared with the null model, for which AIC = 41.27; Table 3). Distance from human habitation had a positive effect on group density, with group density increasing by an estimated

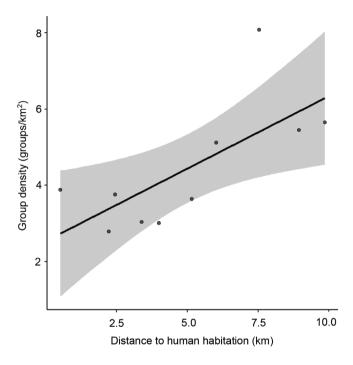


FIGURE 2 Generalized linear model (GLM) predictions (line), with 95% confidence intervals (gray shading), and observed group densities (points) against distance from human habitation (km).

 0.38 ± 0.13 groups/km² with every km of distance (Table 3 and Figure 3).

4 | DISCUSSION

4.1 | Acoustic density surveys

Although accurate and precise density estimates have been obtained for Thomas' langurs previously using visual census methods in several locations within north Sumatra, these were all based on a relatively small number of (often habituated) groups in comparatively small survey areas (between 2 and 4 km²; Table 4). An attempt at surveying unhabituated Thomas' langur groups within the Sikundur area in 2015 using visual census methods yielded no sightings (Slater, 2015), though some groups were heard fleeing from human observers (H. D. Slater, personal observation). Therefore, acoustic surveys where density data can be obtained without the visual presence of humans may greatly aid the precision and accuracy of surveying unhabituated populations over significantly larger geographic areas, as we have found in this study.

Estimated group densities in Sikundur varied from 2.79 to 8.08 groups/km² across the survey area. These density estimates reflect similar estimates obtained from previous studies on habituated groups (Table 4) suggesting acoustic surveys on unhabituated groups can yield accurate density estimates for this species.

The analysis used here is a two-stage modeling approach. Although effective in this instance, an alternative approach is using an all-in-one analysis (Bravington et al., 2021), where the variance propagation as a source of estimate uncertainty is accounted for.

TABLE 2 Mean values for vegetation variables across the 10 survey locations, Gunung Leuser National Park, north Sumatra, March to August 2016.

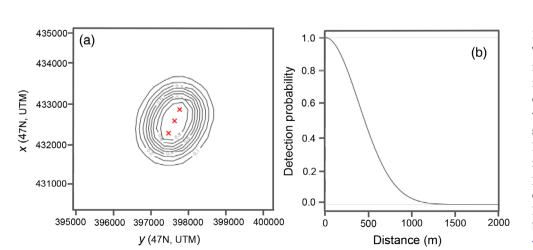
Array location	Estimated density (groups/km²)	Lorey's mean height (m)	Mean bole height (m)	Crown area (m²)	Crown connectivity (%)	Distance to nearest human habitation area (km)
1	3.88	25.53	11.17	84.41	25.00	0.52
2	2.79	31.40	13.25	84.04	27.83	2.23
3	3.76	29.02	14.50	266.84	37.61	2.45
4	3.64	28.41	13.54	199.28	33.58	5.16
5	5.12	22.12	8.71	98.96	22.82	6.02
6	3.01	25.40	9.32	96.68	20.38	4.00
7	3.04	27.92	10.77	85.12	33.26	3.39
8	5.45	30.81	12.75	88.44	30.91	8.94
9	5.65	30.49	9.55	94.49	32.12	9.86
10	8.08	32.44	11.47	83.64	24.78	7.53

4.2 | Thomas' langur densities and vegetation structure

Unlike the two gibbon species (Hylobates lar and Symphalangus syndactylus) residing in the survey location (Hankinson et al., 2021) there was no clear relationship determined between forest structural variables and Thomas' langur group densities in any of the 10 survey locations. This may be due to two possible reasons. First, Thomas' langurs are primarily known as folifrugivores (Sterck & Steenbeek, 1997; Tsuji et al., 2013). This means that this species does not have to locate and exploit scattered fruit sources to the same degree as frugivorous species, as leaves make up a significant part of their diet, potentially reducing their need to travel as far through the canopy. Furthermore, Thomas' langurs are known to spend an increased amount of time traveling on the ground in more secondary forest habitats, and often come down to the ground to drink water and visit mineral sources (Sterck, 1996). Second, Thomas' langurs rest for ~60% of their day to digest leaves and unripe fruit, whereas <10% is spent traveling (Gurmaya, 1986; Sterck, 1996). Thomas' langur

TABLE 3 Coefficient estimates with standard errors in parentheses, Akaike information criterion, and pseudo R^2 values for the best-fit model and null models for the generalized linear model (GLM) with Gaussian distribution testing the effect of distance from human habitation on Thomas' langur group density.

	Best-fit model	Null model
(Intercept)	2.54 (0.78)	4.44 (0.52)
Distance to human habitation, km	0.38 (0.13)	
Ν	10	10
AIC	36.30	41.27
Pseudo R^2	0.51	0.00



average day travel length falls between 0.5 and 1.0 km compared to 1.40 km for lar gibbons and 1.57 km for siamangs (Chivers & Hladik, 1980; Fleagle, 2013; Harrison et al., 2020; MacKinnon, 1977; Savini et al., 2008), this may be a factor in reducing their need for large stretches of well-connected canopy. In addition, there was a large variation in differences in structural vegetation variables between and within measured plots, and the area overall displayed a more heterogeneous gradient of degradation, characteristic of historically logged forests (Struebig et al., 2013), maybe explaining the insignificance of these factors in relation to group densities.

4.3 | Langur density and distance from human habitation

There was a significant positive correlation between Thomas' langur group density and distance from areas of human habitation (Figure 3), supporting our second hypothesis. Human proximity and environmental alteration can affect primate species in several ways, either from direct vegetational damage or through the actual presence of humans. Disturbed and/or secondary forest areas close to human habitation in the Sikundur area are used regularly by local people for fishing and bird trapping (pers. obs.). A previous study on the response of 11 Asian langur species to human presence showed the majority would alarm call loudly and flee upwards into the canopy on approach (two species used crypsis; Nijman & Nekaris, 2012). This was evidenced in Thomas' langurs in Sikundur, where groups were heard vocalizing and fleeing through the canopy on detection (Slater, 2015). This behavior is energetically costly and disrupts natural behaviors leading to decreased time spent foraging, feeding, and resting (Coleman & Hill, 2014; Willems & Hill, 2009). The

> **FIGURE 3** Model output of Thomas langur group densities in acoustic spatial capturerecapture (ASCR) displaying the estimated detection surface where calls are detected (red *x*'s show the location of the listening posts) and detection function (a), and (b) the probability of call detection as distance increases from the listening posts. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 4 Density estimates of Thomas' langur from previous density studies conducted in north Sumatra. For studies with data on group densities or individual densities but without group size data we calculated missing densities using a mean group size of 8.2 langurs: these calculated values are indicated between brackets.

Location	Year(s)	Method	Habitat	Groups recorded	Group size	Group density	Individual density	Reference
Ranau	1971	Mapping of individuals	Alluvial lowland forest	n/a	n/a	[7.8]	64	MacKinnon (1973)
Langkat	1971	Mapping of individuals	Lowland rainforest	n/a	n/a	[2.4]	20	MacKinnon (1973)
Ketambe	1973–1974	Mapping groups and individuals	Alluvial lowland forest	5	9.4	2.9	27	Rijksen (1978)
Bungara	1981–1984	Mapping groups and individuals	Well-managed rubber plantation	9	9.7	2.3	22	Gurmaya (1986)
Bungara	1981–1984	Mapping groups and individuals	Poorly managed rubber plantation	14	7.5	3.9	29	Gurmaya (1986)
Bungara	1981–1984	Mapping groups and individuals	Poorly managed Rubber plantation/ secondary forest	7	6.2	1.9	12	Gurmaya (1986)
Ketambe	1987–1988	Mapping groups and individuals	Alluvial lowland forest	8	7.6-8.9	3.7–7.6	28-68	Assink and van Dijk (1990)
Soraya	2000	Mapping groups and individuals	Hill dipterocarp forest	6	8.2	2.8	23	Syaukani (2012)
Sikundur	2016	Acoustic mapping	Alluvial lowland forest	83	n/a	2.8-8.1	[23-66]	This study
Jantho	2017-2018	Transect walks	Lowland rainforest	7	n/a	0.2–0.7	[2-6]	Ruskhanidar et al. (2020)

Abbreviation: n/a, not available or not recorded.

additional loud alarm calls produced could also attract potential predators such as hawk eagles, a known predator to langurs (Nijman & Nekaris, 2012). Thomas' langurs have been documented as a more tolerant, robust species in comparison to other langurs in terms of structural disturbance caused by logging, spending more time on the ground and living in relatively high densities in plantations (Gurmaya, 1986; Table 4) and therefore in close proximity to humans. However, logging operations have been shown to negatively affect densities of other langur species, such as Hose's Langur (Presbytis hosei) in Borneo (Nijman, 2010). Secondary impacts including decreased food resources, increased susceptibility to infection and parasites as seen in other primate species living close to humans (Foitová et al., 2009; Gillespie & Chapman, 2008; Mbora & Mcpeek, 2009) could also be impacting Thomas' langur densities in Sikundur.

Although this langur species is subjected to hunting pressures in parts of its range, and individuals have been observed being traded in wildlife markets (Shepherd, 2010), Thomas' langurs are not known to be hunted within the Sikundur region (confirmed by locals) and therefore direct hunting pressures are not thought to be a factor in their lower densities in locations close to humans in this study area.

5 | CONCLUSION

Over the last century, human impacts on the natural world, such as large-scale deforestation, have caused huge detrimental effects on the world's tropical forests and the species that reside within them. It is difficult to determine the exact proximate causes to fluctuations in species densities, group sizes and abundance, as many anthropogenic effects can take years before impacts on ecosystems can be seen. Close human habitation within our study location has significantly impacted densities of the Thomas' langur, although the exact reasons for this are unknown, and further study into these would be extremely beneficial. Acoustic surveys and ASCR analysis in this study have shown to be an efficient method in obtaining density estimates over a large geographical area for unhabituated groups, with similar densities obtained to early studies using visual methods. These acoustic methods can aid in population monitoring, allowing species reductions to be monitored, aiding conservation plans and actions, and helping to prevent the future loss of species and ecosystem collapses.

AUTHOR CONTRIBUTIONS

Conceptualization: Amanda H. Korstjens, Ross A. Hill, Emma Hankinson, and Christopher D. Marsh. Data

collection (field): Emma Hankinson, Christopher D. Marsh, Helen D. Slater, and Supradi Supradi. *Data collection (literature)*: Emma Hankinson and Vincent Nijman. *Logistics and facilitation*: Abdullah Abdullah. *Analysis*: Emma Hankinson, Serge A. Wich, Vincent Nijman, Helen D. Slater. *Writing original draft*: Emma Hankinson. *Review and editing*: Amanda H. Korstjens, Ross A. Hill, Emma Hankinson, Christopher D. Marsh, Supradi Supradi, Vincent Nijman, Abdullah Abdullah, NP, Serge A. Wich.

ACKNOWLEDGMENTS

The authors gratefully thank the Ministry of Research, Technology, and Higher Education of the Republic of Indonesia (RISTEKDIKTI, Permit No. 50/SIP/FRP/E5/ Dit.KI/II/2016), the Nature Conservation Agency (BKSDA) and the Gunung Leuser National Park authorities (TNGL) for granting all the necessary permits, which without this research could not have been undertaken. The authors are very grateful for the support and collaboration from Universitas Sviah Kuala, and all staff from the international offices who provided logistical support throughout our time in Indonesia. The authors gratefully acknowledge all researchers and field staff who assisted with the project: Suprayudi Rimba, Ben, Rikki, Wynn, Ucok, and Yangsa who without, various aspects of this field work would not have been possible. The authors would like to thank Dr. Ben Stevenson and Dr. Charlotte Jones-Todd who provided help and advice on the ASCR statistical package.

FUNDING INFORMATION

Funding for this Landscape Ecology and Primatology (LEAP) project was provided by Bournemouth University, and the International Primatological Society (to Christopher D. Marsh). Funding to Sumatran Orangutan Conservation Program's activities at Sikundur was through the Bornean Orangutan Society Canada, US Fish and Wildlife Service, Indianapolis Zoological Association and Philadelphia Zoological Association.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the author on request.

ORCID

Emma Hankinson Dhttps://orcid.org/0000-0001-9708-8587

REFERENCES

- Alempijevic, D., Hart, J. A., Hart, T. B., & Detwiler, K. M. (2022). Using local knowledge and camera traps to investigate occurrence and habitat preference of an Endangered primate: the endemic dryas monkey in the Democratic Republic of the Congo. *Oryx*, 56(2), 260–267.
- Antón Fernández, C. (2019). sitreeE: Sitree extensions. https:// CRAN.R-project.org/package=sitreeE
- Ashbury, A. M., Willems, E. P., Utami Atmoko, S. S., Saputra, F., van Schaik, C. P., & van Noordwijk, M. A. (2020). Home range establishment and the mechanisms of philopatry among female Bornean orangutans (Pongo pygmaeus wurmbii) at Tuanan. *Behavioral Ecology and Sociobiology*, 74(4), 1–21.
- Assink, P., Wich, S., & Steenbeek, R. (1999). Tenure related changes in wild Thomas's langurs II: Loud calls. *Behaviour*, *136*(5), 627–650.
- Assink, P. R., & Van Dijk, I. F. (1990). Social organization, ranging and density of Presbytis thomasi at Ketambe (Sumatra), and a comparison with other Presbytis species at several South-east Asian locations (MSc thesis). University of Utrecht.
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., & Mersey, B. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471(7336), 51–57.
- Barton, K. (2020). MuMIn: Multi-model inference. https://CRAN.Rproject.org/package=MuMIn
- Basyuni, M., Slamet, B., Sulistiyono, N., Thoha, A. S., Bimantara, Y., & Widjaja, E. A. (2019). Species composition and plant diversity of logged-over forest in Sikundur, Gunung Leuser National Park, North Sumatra. *Institute of Physics Conference Series: Earth and Environmental Science* (Vol. 374, No 1, p. 012051). IOP Publishing.
- Batist, C. H., Razafindraibe, M. N., Randriamanantena, F., & Baden, A. L. (2022). Factors affecting call usage in wild blackand-white ruffed lemurs (Varecia variegate) at Mangevo. *Ranomafana National Park. Primates*, 63(1), 79–91.
- Bolt, L. M., Schreier, A. L., Russell, D. G., Jacobson, Z. S., Merrigan-Johnson, C., Barton, M. C., & Coggeshall, E. M. (2019). Howling on the edge: Mantled howler monkey (*Alouatta palliata*) howling behaviour and anthropogenic edge effects in a fragmented tropical rainforest in Costa Rica. *Ethology*, 125(9), 593–602.
- Borchers, D. L., Stevenson, B. C., Kidney, D., Thomas, L., & Marques, T. A. (2015). A unifying model for capture–recapture and distance sampling surveys of wildlife populations. *Journal* of the American Statistical Association, 110, 195–204. https:// doi.org/10.1080/01621459.2014.893884
- Bravington, M. V., Miller, D. L., & Hedley, S. L. (2021). Variance propagation for density surface models. *Journal of Agricultural*, *Biological, and Environmental Statistics*, 26, 306–323.
- Buxton, R. T., Major, H. L., Jones, I. L., & Williams, J. C. (2013). Examining patterns in nocturnal seabird activity and recovery across the Western Aleutian Islands, Alaska, using automated acoustic recording. *The Auk*, 130, 331–341.
- Campbell, G., Head, J., Junker, J., & Nekaris, K. A. I. (2016). Primate abundance and distribution: Background concepts and methods. In S. A. Wich & A. Marshall (Eds.), *An introduction to primate conservation* (pp. 79–110). Oxford University Press.
- Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern

10

human-induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), e1400253.

- Chapman, C. A., Chapman, L. J., Naughton-Treves, L., Lawes, M. J., & Mcdowell, L. R. (2004). Predicting folivorous primate abundance: Validation of a nutritional model. *Ameri*can Journal of Primatology, 62(2), 55–69.
- Cheyne, S. M., Capilla, B. R., Cahyaningrum, E., & Smith, D. E. (2019). Home range variation and site fidelity of Bornean southern gibbons (*Hylobates albibarbis*) from 2010–2018. *PLoS One*, 14(7), e0217784.
- Chivers, D. J., & Hladik, C. M. (1980). Morphology of the gastrointestinal tract in primates: Comparisons with other mammals in relation to diet. *Journal of Morphology*, *166*, 337–386.
- Coleman, B. T., & Hill, R. A. (2014). Living in a landscape of fear: The impact of predation, resource availability and habitat structure on primate range use. *Animal Behaviour*, *88*, 165–173.
- Costa, A., Romano, A., & Salvidio, S. (2020). Reliability of multinomial N-mixture models for estimating abundance of small terrestrial vertebrates. *Biodiversity and Conservation*, 29(9), 2951–2965.
- Dacier, A., de Luna, A. G., Fernandez-Duque, E., & Di Fiore, A. (2011). Estimating population density of Amazonian titi monkeys (*Callicebus discolor*) via playback point counts. *Biotropica*, 43, 135–140.
- Efford, M. G., Dawson, D. K., & Borchers, D. L. (2009). Population density estimated from locations of individuals on a passive detector array. *Ecology*, *90*, 2676–2682.
- Fleagle, J. G. (2013). *Primate adaptation and evolution*. Academic Press.
- Foitová, I., Huffman, M. A., Wisnu, N., & Olsansky, M. (2009). Parasites and their impacts on orangutan health. In Orangutans: Geographic variation in behavioural ecology and conservation (pp. 157–169). Oxford University Press.
- Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., & Heiberger, R. (2012). *Package "car"* (p. 16). R Foundation for Statistical Computing.
- Gibbons, J. W., Scott, D. E., Ryan, T. J., Buhlmann, K. A., Tuberville, T. D., Metts, B. S., Greene, J. L., Mills, T., Leiden, Y., Poppy, S., & Winne, C. T. (2000). The Global Decline of Reptiles, Déjà Vu Amphibians: Reptile species are declining on a global scale. Six significant threats to reptile populations are habitat loss and degradation, introduced invasive species, environmental pollution, disease, unsustainable use, and global climate change. *Bioscience*, 50(8), 653–666.
- Gillespie, T. R., & Chapman, C. A. (2008). Forest fragmentation, the decline of an endangered primate, and changes in host-parasite interactions relative to an unfragmented forest. *American Jour*nal of Primatology: Official Journal of the American Society of Primatologists, 70(3), 222–230.
- Gurmaya, K. (1986). Ecology and behaviour of *Presbytis thomasi* in Northern Sumatra. *Primates*, *27*(2), 151–172.
- Gurmaya, K. J. (1989). Ecology, behaviour and sociality of Thomas' leaf monkey in North Sumatra. *Comparative Primatology Mono*graphs, 2, 53–170.
- Hamard, M., Cheyne, S. M., & Nijman, V. (2010). Vegetation correlates of gibbon density in the peat-swamp forest of the Sabangau catchment, Central Kalimantan, Indonesia. American Journal of Primatology: Official Journal of the American Society of Primatologists, 72(7), 607–616.

- Hankinson, E. L., Hill, R. A., Marsh, C. D., Nowak, M. G., Abdullah, A., Pasaribu, N., Nijman, V., Cheyne, S. M., & Korstjens, A. H. (2021). Influences of forest structure on the density and habitat preference of two sympatric gibbons (*Symphalangus syndactylus* and *Hylobates lar*). *International Journal* of Primatology, 42(2), 237–261.
- Harris, D. V., Miksis-Olds, J. L., Vernon, J. A., & Thomas, L. (2018). Fin whale density and distribution estimation using acoustic bearings derived from sparse arrays. *Journal of the Acoustical Society of America*, 143, 2980–2993.
- Harrison, N. J., Hill, R. A., Alexander, C., Marsh, C. D., Nowak, M. G., Abdullah, A., Slater, H. D., & Korstjens, A. H. (2020). Sleeping trees and sleep related behaviours of the siamang (*Symphalangus syndactylus*) in a tropical lowland rainforest, Sumatra, Indonesia. *Primates*, 62(1), 63–75. https://doi.org/ 10.1007/s10329-020-00849-8
- IUCN (2020). *Red list category summary for all animal classes and orders*. The IUCN Red List of Threatened Species.
- Jones-Todd, C. M. (2019). ASCR user interface package. https:// cmjt.shinyapps.io/ascr_shiny/
- Kidney, D., Rawson, B., Borchers, D. L., Stevenson, B. C., Marques, T. A., & Thomas, L. (2016). An efficient acoustic density estimation method with human detectors applied to gibbons in Cambodia. *PLoS One*, *11*, e0155066.
- Klaus, A., Strube, C., Röper, K. M., Radespiel, U., Schaarschmidt, F., Nathan, S., Goossens, B., & Zimmermann, E. (2018). Faecal parasite risk in the endangered proboscis monkey is higher in an anthropogenically managed forest environment compared to a riparian rain forest in Sabah, Borneo. *PLoS One*, 13(4), e0195584.
- Klinck, H., Mellinger, D. K., Klinck, K., Bogue, N. M., Luby, J. C., Jump, W. A., Shilliing, G. B., Litchendorf, T., Wood, A. S., Schorr, G. S., & Baird, R. W. (2012). Near-real-time acoustic monitoring of beaked whales and other cetaceans using a Seaglider[™]. *PLoS One*, 7, e361282012.
- Knop, E. (2004). A comparison of orang-utan density in a logged and unlogged forest on Sumatra. *Biological Conservation*, 120(2), 183–188.
- Lambert, K. T., & McDonald, P. G. (2014). A low-cost, yet simple and highly repeatable system for acoustically surveying cryptic species. *Austral Ecology*, *39*(7), 779–785.
- Lee, D. C., Powell, V. J., & Lindsell, J. A. (2015). The conservation value of degraded forests for agile gibbons (*Hylobates agilis*). *American Journal of Primatology*, 77(1), 76–85.
- Lonsdorf, E. V., Stanton, M. A., Pusey, A. E., & Murray, C. M. (2020). Sources of variation in weaned age among wild chimpanzees in Gombe National Park, Tanzania. *American Journal* of *Physical Anthropology*, 171(3), 419–429.

MacKinnon, J. (1973). Orangutans in Sumatra. Oryx, 12(2), 234-242.

- MacKinnon, J. (1977). A comparative ecology of Asian apes. Primates, 18, 747-772.
- Manullang, B. O. (1999). Distribution patterns of Sumatran plants and primates. University of California.
- Marques, T. A., Thomas, L., Martin, S. W., Mellinger, D. K., Ward, J. A., Morettie, D. J., Harris, D., & Tyack, P. L. (2013). Estimating animal population density using passive acoustics. *Biological Reviews*, 88, 287–309.
- Mbora, D. N., & McPeek, M. A. (2009). Host density and human activities mediate increased parasite prevalence and richness in

WILEY- RESEARCH

primates threatened by habitat loss and fragmentation. *Journal* of Animal Ecology, 78(1), 210–218.

- Measey, G. J., Stevenson, B. C., Scott, T., Altwegg, R., & Borchers, D. L. (2017). Counting chirps: Acoustic monitoring of cryptic frogs. *Journal of Applied Ecology*, 54, 894–902.
- Neilson, E., Nijman, V., & Nekaris, K. A. I. (2013). Conservation assessments of arboreal mammals in difficult terrain: Occupancy modelling of Pileated Gibbons (*Hylobates pileatus*). *International Journal of Primatology*, 2013(34), 823–835.
- Nijman, V. (2010). Ecology and conservation of the Hose's Langur Group Colobinae: Presbytis hosei, P. canicrus, P. sabana: A review. In S. Gursky-Doyen & J. Supriatna (Eds.), Indonesian primates (pp. 269–284). Springer.
- Nijman, V. (2021). Ecology of sympatric and allopatric *Presbytis* and *Trachypithecus* langurs in Sundaland. In I. Matsuda & C. C. Grueter (Eds.), *The colobines: Natural history, behaviour and ecological diversity*. Cambridge University Press.
- Nijman, V., & Nekaris, K. A. I. (2012). Loud calls, startle behaviour, social organisation and predator avoidance in arboreal langurs (Cercopithecidae: Presbytis). *Folia Primatologica*, *83*(3–6), 274–287.
- Phoonjampa, R., Koenig, A., Brockelman, W. Y., Borries, C., Gale, G. A., Carroll, J. P., & Savini, T. (2011). Pileated gibbon density in relation to habitat characteristics and post-logging forest recovery. *Biotropica*, 43(5), 619–627.
- Plumptre, A. J., Sterling, E. J., & Buckland, S. T. (2013). Primate census and survey techniques. In *Primate ecology and conservation: A handbook of techniques* (pp. 10–26). Oxford University Press.
- Priatna, D., Kartawinata, K., & Abdulhadi, R. (2004). Recovery of a lowland dipterocarp forest twenty-two years after selective logging at Sekundur, Gunung Leuser National Park, North Sumatra, Indonesia. *Reinwardtia*, 12, 237–255.
- Reed, K. E., & Bidner, L. R. (2004). Primate communities: Past, present, and possible future. *American Journal of Physical Anthropology*, 125(S39), 2–39.
- Rijksen, H. D. (1978). A field study on Sumatran orang utans (Pongo pygmaeus abelii Lesson 1827): ecology, behaviour and conservation. Wageningen University and Research.
- Roffler, G. H., Waite, J. N., Pilgrim, K. L., Zarn, K. E., & Schwartz, M. K. (2019). Estimating abundance of a cryptic social carnivore using spatially explicit capture-recapture. *Wildlife Society Bulletin*, 43(1), 31–41.
- Roth, T. S., Rianti, P., Fredriksson, G. M., Wich, S. A., & Nowak, M. G. (2020). Grouping behaviour of Sumatran orangutans (*Pongo abelii*) and Tapanuli orangutans (*Pongo tapanuliensis*) living in forest with low fruit abundance. *American Journal* of *Primatology*, 82(5), e23123.
- Ruskhanidar, R., Alikodra, H. S., Iskandar, E., Santoso, N., & Mansjoer, S. S. (2020). Analisis populasi kedih (*Presbytis thomasi*) di cagar alam pinus jantho ACEH besar provinsi ACEH. *Journal Penelitian Hutan dan Konservasi Alam*, 17(2), 207–220.
- Savini, T., Boesch, C., & Reichard, U. H. (2008). Home-range characteristics and the influence of seasonality on female reproduction in white-handed gibbons (*Hylobates lar*) at Khao Yai National Park, Thailand. *American Journal of Physical Anthropology*, 135(1), 1–12.
- Sebastián-González, E., Camp, R. J., Tanimoto, A. M., de Oliveira, P. M., Lima, B. B., Marques, T. A., & Hart, P. J. (2018). Density estimation of sound-producing terrestrial animals

using single automatic acoustic recorders and distance sampling. Avian Conservation and Ecology, 13, 7.

- Setiawan, A., & Traeholt, C. (2020). Presbytis thomasi. The IUCN Red List of Threatened Species 2020: e.T18132A17954139. https://doi.org/10.2305/IUCN.UK.2020-2.RLTS.T18132A179541 39.en
- Shepherd, C. R. (2010). Illegal primate trade in Indonesia exemplified by surveys carried out over a decade in North Sumatra. *Endangered Species Research*, 11, 201–205.
- Slater, H. D. (2015). Forest structure and group density of Thomas' langur monkey, *Prebytis thomasi* [Unpublished Master's Thesis]. Bournemouth University, UK.
- Steenbeek, R. (1999). Tenure related changes in wild Thomas's langurs I: Between-group interactions. *Behaviour*, 136, 595–625.
- Steenbeek, R., & van Schaik, C. P. (2001). Competition and group size in Thomas's langurs (*Presbytis thomasi*): The folivore paradox revisited. *Behavioural Ecology and Sociobiology*, 49(2), 100–110.
- Sterck, E. H. (1999). Variation in langur social organization in relation to the socioecological model, human habitat alteration, and phylogenetic constraints. *Primates*, 40(1), 199–213.
- Sterck, E. H., & Steenbeek, R. (1997). Female dominance relationships and food competition in the sympatric Thomas' langur and long-tailed macaque. *Behaviour*, 134(9–10), 749–774.
- Sterck, E. H. M. (1996). The langurs of Gunung Leuser National Park (pp. 281–294). Leuser—A Sumatran sanctuary.
- Sterck, E. H. M., Willems, E. P., Van Hooff, J. A., & Wich, S. A. (2005). Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). *Behaviour*, 142, 845–868.
- Stevenson, B. C., Borchers, D. L., Altwegg, R., Swift, R. J., Gillespie, D. M., & Measey, G. J. (2015). A general framework for animal density estimation from acoustic detections across a fixed microphone array. *Methods in Ecology and Evolution*, 6, 38–48.
- Stevenson, B. C., van Dam-Bates, P., Young, C. K. Y., & Measey, J. (2020). A spatial capture–recapture model to estimate call rate and population density from passive acoustic surveys. *Methods in Ecology and Evolution*, 12(3), 432–442.
- Struebig, M. J., Turner, A., Giles, E., Lasmana, F., Tollington, S., Bernard, H., & Bell, D. (2013). Quantifying the biodiversity value of repeatedly logged rainforests: Gradient and comparative approaches from Borneo. In *Advances in ecological research* (Vol. 48, pp. 183–224). Academic Press.
- Syaukani, S. (2012). Study of population and home range of Thomas langur (*Presbytis thomasi*) at Soraya Research Station, Leuser Ecosystem. *Journal Natural*, 12(1), 37–41.
- Tsuji, Y., Hanya, G., & Grueter, C. C. (2013). Feeding strategies of primates in temperate and alpine forests: Comparison of Asian macaques and colobines. *Primates*, 54(3), 201–215.
- Turubanova, S., Potapov, P. V., Tyukavina, A., & Hansen, M. C. (2018). Ongoing primary forest loss in Brazil, Democratic Republic of the Congo, and Indonesia. *Environmental Research Letters*, 13(7), 074028.
- Ungar, P. S. (1994). Incisor microwear of Sumatran anthropoid primates. American Journal of Physical Anthropology, 94(3), 339–363.
- Ungar, P. S. (1995). Fruit preferences of four sympatric Primate species at Ketambe, northern Sumatra, Indonesia. *International Journal of Primatology*, 16(2), 221–245.

- Ungar, P. S. (1996). Feeding height and niche separation in sympatric Sumatran monkeys, feeding height and niche separation in sympatric Sumatran monkeys and apes and apes. *Folia Primatologica*, *67*(3), 163–168.
- Van Schaik, C. P., Van Noordwijk, M. A., Warsono, B., & Sutriono, E. (1983). Party size and early detection of predators in Sumatran forest primates. *Primates*, 24(2), 211–221.
- Voigt, M., Wich, S. A., Ancrenaz, M., Meijaard, E., Abram, N., Banes, G. L., Campbell-Smith, G., d'Arcy, L. J., Delgado, R. A., Erman, A., & Gaveau, D. (2018). Global demand for natural resources eliminated more than 100,000 Bornean orangutans. *Current Biology*, 28(5), 761–769.
- Vu, T. T., & Rawson, B. M. (2011). Package for calculating gibbon population density from auditory surveys. Conservation International and Fauna & Flora International.
- Vu, T. T., Tran, L. M., Nguyen, M. D., Van Tran, D., & Ta, N. T. (2018). Improving the estimation of calling probability and correction factors in gibbon monitoring using the auditory point count method. *International Journal of Primatology*, 39(2), 222–236.
- Wich, S. A., Assink, P. R., & Sterck, E. H. M. (2004). Thomas langurs (*Presbytis thomasi*) discriminate between calls of young solitary versus older group-living males: A factor in avoiding infanticide. *Behaviour*, 141(1), 41–52.
- Wich, S. A., & De Vries, H. (2006). Male monkeys remember which group members have given alarm calls Royal Society of London. *Proceedings Biological Sciences*, 273(1587), 735–740.
- Wich, S. A., Schel, A. M., & De Vries, H. (2008). Geographic variation in Thomas langur (*Presbytis thomasi*) loud calls. *American Journal of Primatology: Official Journal of the American Society* of Primatologists, 70(6), 566–574.
- Wich, S. A., Steenbeek, R., Sterck, E. H. M., Korstjens, A. H., Willems, E. P., & van Schaik, C. P. (2007). Demography and life history of Thomas langurs (*Presbytis thomasi*). *American Journal of Primatology*, 69, 641–651.
- Wich, S. A., & Sterck, E. H. (2010). Thomas langurs: Ecology, sexual conflict and social dynamics. In S. Gursky-Doyen & J. Supriatna (Eds.), *Indonesian primates* (pp. 285–308). Springer.

- Wich, S. A., & Sterck, E. H. M. (2003). Possible audience effect in Thomas langurs primates (*Presbytis thomasi*): An experimental study on male loud calls in response to a tiger model. *American Journal of Primatology: Official Journal of the American Society* of Primatologists, 60(4), 155–159.
- Wich, S. A., Van der Post, D. J., Heistermann, M., Möhle, U., Van Hooff, J. A. R. A. M., & Sterck, E. H. M. (2003). Life-phase related changes in male loud call characteristics and testosterone levels in wild Thomas langurs. *International Journal of Primatology*, 24(6), 1251–1265.
- Willems, E., & Hill, R. (2009). Predator-specific landscapes of fear and resource distribution: Effects on spatial range use. *Ecology*, 90(2), 546–555. https://doi.org/10.1890/08-0765.1
- Wilson, C. C., & Wilson, W. L. (1976). Behavioural and morphological variation among primate populations in Sumatra. *Yearbook* of *Physical Anthropology*, 20, 207–233.
- Wrege, P. H., Rowland, E. D., Keen, S., & Shiu, Y. (2017). Acoustic monitoring for conservation in tropical forests: Examples from forest elephants. *Methods in Ecology and Evolution*, 8(10), 1292–1130.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Hankinson, E.,

Korstjens, A. H., Hill, R. A., Wich, S. A., Slater, H. D., Abdullah, A., Supradi, S., Marsh, C. D., & Nijman, V. (2022). Effects of anthropogenic disturbance on group densities of Thomas' langurs (*Presbytis thomasi*) within a lowland tropical forest, north Sumatra. *Ecological Research*, 1–13. <u>https://</u> <u>doi.org/10.1111/1440-1703.12373</u>