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Estimating densities and spatial distribution of a commensal primate species, the long-tailed macaque (*Macaca fascicularis*)

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Abstract

Knowledge about distribution of primate species and their densities is crucial for conservation and management. However, such information is often lacking or anecdotal, even for seemingly abundant species. Long-tailed macaques (*Macaca fascicularis*) are distributed across southeast Asia and recognized by the International Union for Conservation of Nature Species Survival Commission Primate Specialist Group (IUCN SSC PSG) as both widespread and rapidly declining. Precise local density and abundance data are scarce across their range. To provide density and abundance estimates for a long-tailed macaque population we conducted line transect distance sampling throughout Baluran National Park (250 km^2), East Java, Indonesia covering all habitats. Long-tailed macaque density was 41.4 ind/km^2 (95% confidence interval, CI: 23.04–74.39), with an estimated abundance of 10,350 individuals (95% CI: 5,760–18,598). A density of 41.4 ind/km^2 is lower than previous estimates for other sites in Java. Species distribution and habitat suitability analysis revealed a macaque preference for areas close to or on roads and trails, invasive acacia and/or native savannah. Long-tailed macaques were provisioned with human food by commuters and tourists along roads and trails, probably structuring their distribution/habitat use. To evaluate if long-tailed-macaques have been overestimated for years, we also conducted a nonrandom point distance sampling survey according to macaque presence restricted to roads and trails. This survey provided density and abundance results much higher than the line transect distance sampling survey. Our study provides much needed baseline data for this species. Baluran National Park management and management in other areas can use these results to create informed management decisions regarding long-tailed macaques. We recommend conducting systematic surveys of long-tailed macaques throughout their range, and possibly reassessing conservation status, and conservation and management measures for long-tailed macaques.

KEYWORDS
abundance, line transect, management, point distance sampling, protected areas, species distribution models, systematic

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1 | INTRODUCTION

The 2018 assessment of primates in peril concluded that 83% of Indonesian primate species are threatened, and 94% are declining (Estrada et al., 2018). Human activities are considered the main reason for this decline and subsequent likely species extinctions (Estrada et al., 2017). Baluran National Park (BNP), East Java, Indonesia is a protected area under Indonesian law, and an IUCN Protected Area Management (Cat II), yet is experiencing many threats such as invasive African acacia and domestic cattle (Pudyatmoko, 2017; Setiabudi, Tjitrosoedirdjo, Tjitrosoedirdjo, Mawardi, & Bachri, 2013; UNEP-WCMC, 2018; Wianti, 2014). Moreover, provisioning of long-tailed macaques (*Macaca fascicularis*) with human food both indirectly and directly is widespread in the park and may affect the ecology of the species, leading to increased population sizes in tourist areas (Hansen, Wahyudi, Supriyanto, & Damanik, 2015). This occurs on the regional road running through the park, in tourist areas inside the park, near and around settlements inside the park, and in agricultural areas inside and around the park. The level of provisioning changes according to human density (commuters and national park visitors), and seasonality of crops (Hansen et al., 2015 and own observations). The ecological flexibility of long-tailed macaques enables them to adapt to food availability (Gumert, Fuentes, & Jones-Engel, 2011), and BNP macaques seems to experience high behavioral plasticity with groups ranging from nonprovisioned to semi-provisioned to highly provisioned (Hansen et al., n.d.). All groups experiencing provisioning also forage outside anthropogenic areas to different degrees. This behavioral flexibility has complicated population assessments in the past. To foster conservation initiatives and management plans for wildlife, accurate information on population density and abundance is essential (Buckland et al., 2001; Dice, 1938). However, such data are currently lacking for BNP, which limits successful conservation management.

Long-tailed macaques are widespread across southeast Asia, and have the ability to exploit many different habitats, including those with anthropogenic disturbance such as agriculture, urbanized recreation parks, and temples (Fooden, 1995; Fuentes et al., 2008; Gumert et al., 2011; Muroyama & Eudey, 2004). Long-tailed macaques are listed as Least Concern on the IUCN Red List (Ong & Richardson, 2008), and recognized as widespread, yet rapidly declining (Eudey, 2008). Conflicts with humans, trade for the medical industry, and pet trade has resulted in their decline (Eudey, 2008). The trade for the medical industry and the pet trade in long-tailed macaques is heavy and unregulated, and in many instances long-tailed macaques are harvested directly from the wild (Foley & Shepherd, 2011). This may be unsustainable and

causing a population decline (Foley & Shepherd, 2011). Cambodia exports long-tailed macaques for medicinal trade (Foley & Shepherd, 2011), and long-tailed macaques here have always been viewed as abundant, but a recent survey of several sites in Cambodia including suitable natural habitats and meat markets, found no monkeys (Lee, 2011). There is a growing concern for their survival, and some even fear that they will face the same fate as the passenger pigeon (Eudey, 2008; Gumert et al., 2011; C. van Schaik, R. Mittermeier, & I. Redmond, personal communication, August 24, 2018). Even abundant species can be driven to extinction, or decline quickly, such as the passenger pigeon (*Ectopistes migratorius*)—extinct in 1914 (Schorger, 1955), and the bonnet macaque (*Macaca radiata*)—65% decline over the past 25 years (Erinjery et al., 2017).

Detailed data on the distribution, density, and abundance of long-tailed macaques are lacking (Eudey, 2008; Kyes, Iskander, & Pamungkas, 2011; Muroyama & Eudey, 2004), and existing data have been collected mostly from provisioned populations (Table 1). Most data from nonprovisioned populations are from the 1990s (Table 1), and some were not collected in a scientifically rigorous manner. In 2009, a survey of the distribution of long-tailed macaques in Java found that long-tailed macaques were absent from many areas across Java, including suitable forest areas, and that their visibility in human areas may have led to overestimation of their population size (Kyes et al., 2011).

This study aims to provide the first quantification of density, abundance, and habitat suitability of long-tailed macaques in BNP, and hereby the first for the island of Java. We employ line transect distance sampling (LTDS), which has proven successful for surveying many species of terrestrial mammals, including primates (Buckland et al., 2001; Buckland, Plumptre, Thomas, & Rexstad, 2010; Peres, 1999), and species distribution modelling (SDM), which is increasingly used to quantify habitat suitability for wildlife, and is useful for conservation planning (Bellamy, Scott, & Altringham, 2013; Nüchel, Bøcher, Xiao, Zhu, & Svenning, 2018; Pearson, Raxworthy, Nakamura, & Townsend Peterson, 2007). Our methods will provide baseline data and enable habitat assessment and management and conservation initiatives (Bellamy et al., 2013; Plumptre & Cox, 2006).

In addition to our LTDS survey, we also include a nonrandom point distance sampling (PDS) survey on roads and trails to compare density estimates to our LTDS results to assess if long-tailed macaques have been overestimated across their range. In BNP and in other areas, long-tailed macaque populations have often been estimated by counting individuals at roads and trails in a nonrandomized design, counting from points placed according to animal distribution and extrapolating this to other habitats in the same area (Sha et al., 2009). This can lead to bias in population estimates

TABLE 1 Group size, density and sex ratio (male:female) of long-tailed macaque populations across their range

Area	Provisioned	Density (ind/km²)	Group size	Sex ratio (M:F)
Southeast Asia mean[1]	No	55	—	—
Southeast Asia mean[1]	Yes	100	—	—
Singapore	Semi[2,8]	0.89–33.63[2,8]	24.2 ± 9.85[2]	0.55:1[2]
Bali, Indonesia	Yes	555[3]–5850[5]	198[3]	0.26–0.32:1[3]
Bali, Indonesia[3]	No	70	25	0.43:1
Sumatra, Indonesia	No	9.9[6]–143.4[1]	6–65[1,4,6]	0.90:1[1]
Java	No	41.4[9]–55[1]	39–61[1,9]	0.83[1]–0.89[9]:1
Vietnam[7]	Yes	67	26–170	—

Note: Compiled by [1]Fooden (1995), [2]Riley, Jayasri, and Gumert (2015), [3]Brotcorne (2014), [4]van Schaik, van Noordwijk, Boer, and den Tonkelaar (1983), [5]Wheatley (1989), [6]Yanuar, Chivers, Sugardjito, Martyr, and Jeremy (2009), [7]Son (2004), [8]Sha et al. (2009), [9]This study (Table 2, Table S1, and Hansen et al., n.d.).

(Marques, Buckland, Borchers, Tosh, & McDonald, 2010), as long-tailed macaques are not uniformly distributed across habitats, often experiencing a higher density on roads and trails.

2 | METHODS

2.1 | Study site

BNP is located at the northeast tip of Java in Indonesia (7°50′0″S, 114°22′0″E) and encompasses 250 km² of a wide variety of habitats, including primary and secondary forest, savannah, and mangroves (Figure 1; Pudyatmoko, Budiman, & Kristiansen, 2018; Siswanto, 2015). The national park was gazetted in 1980 including already established settlements (Wianti, 2014). Species richness of wild mammals in the area has been negatively affected since the beginning of the settlements in 1975, especially due to the over 4,000 domestic cattle that graze the northern Merak savannah daily (Pudyatmoko et al., 2018; Wianti, 2014). The Merak savannah is the only large area of native savannah left in BNP, and grazing cattle entering from Merak village reach as far as savannah habitats on the northern and eastern lower parts of Baluran Mountain (Figure 1).

African acacia (*Acacia nilotica*) has invaded the native savannah since it was introduced in 1969 (Padmanaba, Tomlinson, Hughes, & Corlett, 2017; Setiabudi et al., 2013). Human encroachment, land conversion, and invasive species leaves BNP in need of extensive management efforts in order to conserve the biodiversity (Padmanaba et al., 2017; Pudyatmoko, 2017; Pudyatmoko et al., 2018).

BNP is open for tourists year-round in designated areas and is traversed by a highway in the southwest. Visitors and commuters frequently engage in provisioning of long-tailed macaques, despite such behavior being prohibited by park regulations. The national park staff does not officially feed the macaques (Hansen et al., 2015). When encountering long-tailed macaques outside areas of provisioning they often exhibit a larger flight distance than in anthropogenic areas. Poaching does occur in BNP, and humans outside provisioning areas may be perceived as threats by the long-tailed macaques.
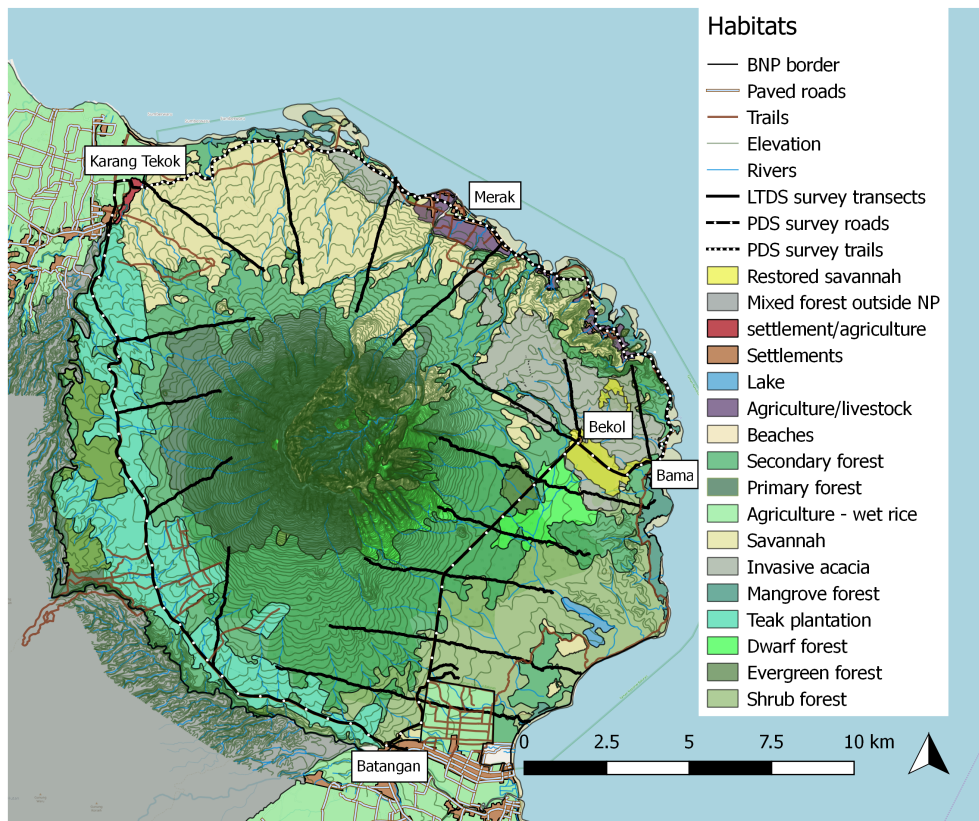
2.2 | Data collection

We did not capture, handle, or harm any animals during this study.

2.2.1 | Line transect distance sampling

Twenty-one line transects were placed throughout the park beginning at roads or trails and covering all habitat types (Figure 1). We followed all key assumptions of LTDS as outlined in Buckland et al. (2001, 2010). For safety and logistical reasons we did not include Baluran Mountain at the center of the park in the survey design. Anecdotal evidence from park rangers suggests that the population there is small, with few groups numbering ~5 ind/group.

Transects were placed with a minimum of 2 km between adjacent transects at the nearest points (Figure 1), creating a grid of transects which is systematic in structure but random in respect to habitats and animal distribution (Buckland, Rexstad, Marques, & Oedekoven, 2015). Transects were 4.5 km long, totaling 94.5 km of transect lines. All transects were walked once; outbound (7 a.m.–11 a.m.) and return (1 p.m.–5 p.m.). Walking speed was approximately 1.2 km/hr as recommended by Peres (1999). We detected animals via sight and/or vocalizations, and began counting when they were visible (Plumptre & Cox, 2006). This will be termed as an observation from now on. Observations never exceeded 15 min, aiming at never letting animals move ahead of us to avoid double-counting (Buckland et al., 2010). We only walked one transect at a time, and aimed at detecting all animals at zero distance (Buckland et al.,

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FIGURE 1 Above: QGIS BING aerial map of BNP, Java, Indonesia, and the islands surrounding it. Below: QGIS map of Baluran National Park with walked and driven transects, roads and trails track vectors, and habitat rasters. Surroundings consists of villages and wet rice (south and northwest), the Bali Strait (east) and unprotected mixed forest and agriculture (west)

2010). We used a Garmin GPS Map 64s (Garmin) to keep our bearing, find the perpendicular point and waypoint the position. We then measured the perpendicular distance (PD) to sub-group center using a Nikon Aculon A11 Rangefinder (Nikon), and counted sub-group size using repeated counts, where all observers counted repeatedly within the 15 min until consensus (Peres, 1999; Ross & Reeve, 2003). We recorded PD to center of measurable individuals (sub-groups) at their initial location of detection (Plumptre & Cox, 2006). Sub-groups are smaller foraging units where group center is easily estimated, and bias in PD reduced. Measuring the PD directly to estimated sub-group center is as accurate as correcting for group spread (Plumptre & Cox, 2006). We moved around small obstacles to minimize cutting, but always measured distance to sub-groups from the line if possible (Buckland et al., 2010). We recorded age and sex groups where possible: adult males (>6 years), adult females (>3.5 years), sub-adult males (4–6 years), juveniles (1–4 years), infants (0–1 years) (Brotcorne, 2014; van Schaik et al., 1983).

We conducted the survey from October 16, 2017 to December 2, 2017 at the end of dry season and the beginning of wet season, which is the only time of year that most habitats are accessible. We created a transect grid that was random according to habitat and animal distribution enabling nonbiased density and abundance estimates irrespective of season.

2.2.2 | Point distance sampling

The PDS survey design was created to investigate if the historic and current assumption of assessing a commensal species only by its distribution in anthropogenic areas is viable and to mirror previous studies that were restricted to counting at edges (Riley et al., 2015). Results were therefore not a true picture of the population size of long-tailed macaques in BNP, and only included for comparison with the LTDS survey, and to urge management and researchers to reconsider their population survey methods. We conducted nonrandom PDS on the highway Jalan Raya Banyuwangi, Situbondo between the Batangan entrance and Karangtekok entrance, and on the tourist road going from Batangan entrance to Bekol tourist site to Bama tourist site, and the trail going from Bama tourist site to Merak village to Karangtekok entrance (Figure 1). Combined roads and trails comprised 54 km inside the outermost parts of the park. We drove on roads and trails, and stopped when encountering sub-groups of macaques, registered our GPS position (our point on the road or trail), measured radial distance to sub-group center, and counted the individuals of the sub-group until consensus. We only visited points once. The PDS survey was conducted in November 2017.

2.3 | Data analysis

2.3.1 | Line transect distance sampling

LTDS observations were analyzed in Distance 7.1 (Thomas et al., 2010). We only included outbound observations for the density and abundance analysis to avoid double-counts. Abundance was estimated according to total national park area: 250 km^2. We could not measure accurate PD for eight sightings of macaques. These observations were excluded from all analysis but included in Table S1.

We chose to right truncate data to exclude all observations beyond 90 m to increase robustness in estimating detection function (Buckland et al., 2001), removing 3 out of 73 observations. The truncation distance was determined by investigating histograms of the data without truncation (E. Rextad & T. Marques, personal communication, 2018). We saw a drop in sightings after 90 m, yet had sightings up to 250 m away. We expect the difference in sighting distance to be due to the difference in habitats, which ranged from open savannah to dense shrub forest (Figure 1). We tested all available combinations of detection functions and adjustments on our data to find the best-fit according to lowest Akaike Information Criterion (AIC), best goodness of fit (GOF) tests and lowest χ^2/df accumulated for χ^2 tests (Buckland et al., 2001; Thomas et al., 2010; Figure S1).

2.3.2 | Map of Baluran

We created a map of BNP in QGIS 2.18.19 (Creative Commons) with shapefiles containing raster layers provided by BNP, and updated it according to contemporary Google Earth features. We inserted vector layers from our tracks from the LTDS and the PDS surveys.

2.3.3 | Environmental predictors for species distribution modelling

Thirty-nine raster layers (15 × 15-m resolution) were generated as potential environmental predictor variables for SDM habitat suitability using the raster package in R (Hijmans, 2017). Topographic layers ($n = 5$) included elevation (m), slope (°), aspect (radians), hill-shade (radians) and terrain ruggedness (index), which were derived from a digital elevation model of the study area (provided by BNP). Using ESRI shapefiles, we generated a raster layer that included 13 major vegetation/habitat types found in the study area including: rice fields, livestock fields, teak plantations, dwarf forests, evergreen forest, shrub forest, primary forest, secondary forest, mangroves, acacia forest, savannah, restored savannah, and beach. We then created new raster layers, where for each 15 × 15-m pixel the Euclidean distance (km) to each vegetation type ($n = 13$) was calculated, as well as the % cover of

each vegetation type within an 1 km^2 grid layer placed over the study area ($n = 13$). We used the distance and density rasters instead of the categorical raster for habitat/vegetation types as the former two metrics are better able to capture potential edge effects in habitat suitability. The last eight raster layers comprised both Euclidian distance to (km) and density of (km^2) paved roads, human settlements, trails, and rivers found in the study area.

Collinearity among explanatory variables may increase the probability of Type I and/or Type II errors. Therefore, we continued using raster layers with either the distance variables or the % cover variables, alongside environmental layers not related to vegetation type. For each set of variables we further excluded collinear raster layers using a stepwise procedure by calculating Varience Inflation Factor (VIF) and excluding the highest VIF until only layers with a VIF <3 remained (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014). This procedure led to the inclusion of 11 covariates when considering the distance to vegetation type layers and to the inclusion of 14 covariates when considering the % cover of vegetation type layers.

2.3.4 | Species distribution modelling, evaluation, and mapping

SDM and mapping of habitat suitability were conducted using the SDM package in R (Naimi & Araújo, 2016). We initially ran eight model algorithms to test which methods provided the best-fit with the data by evaluating model accuracy based on the area under the curve (AUC) of the receiver operating characteristic (Fielding & Bell, 1997). Initial analyses revealed that MaxEnt performed the best with the highest AUC value, and we will only present results from this model. Projected waypoints of observations from both the outbound and return trip of each transect from the LTDS population survey were used as presence locations ($N = 103$). Values of environmental conditions for presence points were extracted from all noncorrelated environmental raster layers. However, we ran separate models considering either the distance to vegetation types or % cover of vegetation types as predictor variables. For each run, we partitioned the data into 70% training and 30% testing to assess model performance because independent data were not available. Ten models were computed using a bootstrap procedure. An AUC value of 0.5 indicates that the model performs no better than a random model, whereas a value of 1 indicates perfect performance. AUC values of >0.7 typically indicate good model accuracy (Pearson et al., 2006). Finally, we evaluated variable importance by calculating the change in the AUC value (ΔAUC) with and without a specific environmental variable, but with all other variables included. We visualized the variable importance of environmental conditions as determined by ΔAUC.

2.3.5 | Point distance sampling

PDS observations were analyzed using Distance 7.1 (Thomas et al., 2010). We recorded 22 observations of long-tailed macaque sub-groups equaling 22 samples (points). After 5% truncation, 21 observations remained for the analysis. We tested several detection functions, and chose the one with lowest AIC and best GOF test (Buckland et al., 2001; Figure S2). We estimated the PDS abundance for roads and trails, and under the assumption that density was constant across the park, we also estimated abundance for the entire park. Estimated survey area for roads and trails was calculated as 16.2 km^2; 54 km × 300 m. We chose 150 m as the radius from the center of the road, because our radial distance for detections never exceeded this.

3 | RESULTS

Out of the 189 km transects planned of the LTDS, we surveyed a combined 160.56 km for the 21 transects. Transect length varied from 3 to 5 km per transect depending on accessibility (Figure 1).

We encountered an almost equal number of individuals in the two surveys (Table S1). More adult males and juveniles to every female were encountered on the LTDS survey, than in the PDS survey.

3.1 | LTDS density and abundance estimation

The density of long-tailed macaques in the entire national park was estimated to be 41.4 ind/km^2 with a *SE* of 12.31 and a coefficient of variation of 29.74% and a 95% confidence interval (CI) ranging from 23.04 to 74.39 ind/km^2 (Table 2). The estimated total population size for the national park was 10,350 long-tailed macaques with a 95% CI of 5,760–18,598 ind (Table 2). Estimated sub-group density was 10.87 groups/km^2 and estimated sub-group size mean was 3.81 ind (Table 2).

3.2 | Habitat suitability

The model with distance to vegetation types as covariates consistently outperformed the model with percentage cover of vegetation types. For completeness, we provide the habitat suitability map of percentage cover of vegetation types in Figure S3. Considering the distance-based covariates, MaxEnt performed well with a mean AUC of 0.86, and min and max were 0.82 and 0.90, respectively, as calculated over 10 runs.

TABLE 2 Density and abundance estimates for long-tailed macaques from Distance 7.1, half normal key, two cosine adjustments, 90 m truncation, AIC

Parameter	Estimate	SE	%CV	df	95% CI
DS	10.87	2.98	27.40	33	6.29–18.79
E(S)	3.81	0.44	11.56	63	3.03–4.79
D	41.4	12.31	29.74	46	23.04–74.39
N	10,350	3,077.8	29.74	46	5,760–18,598

Note: AIC, Akaike Information Criterion; CI, confidence interval; CV, coefficient of variation; D, estimate of density of individuals (number per km^2); DS, estimate of density of groups (number per km^2); df, degrees of freedom; E(S), estimate of expected value (mean) of group size; N, abundance estimate.

Distance to roads, distance to acacia (invasive), distance to savannah, and distance to shrub forest had the highest variable importance, and all over or equal to 0.1 (Figure 2) for the habitat suitability map. Distance to rivers and hill shade had the lowest variable importance (Figure 2).

The habitat suitability map highlights several areas with high preference for long-tailed macaques. Many are anthropogenic (Figure 3).

3.3 | PDS density and abundance estimation

All results are presented in Table 3. Estimated density from the PDS survey was 1,407.6 individuals larger per square kilometer than the estima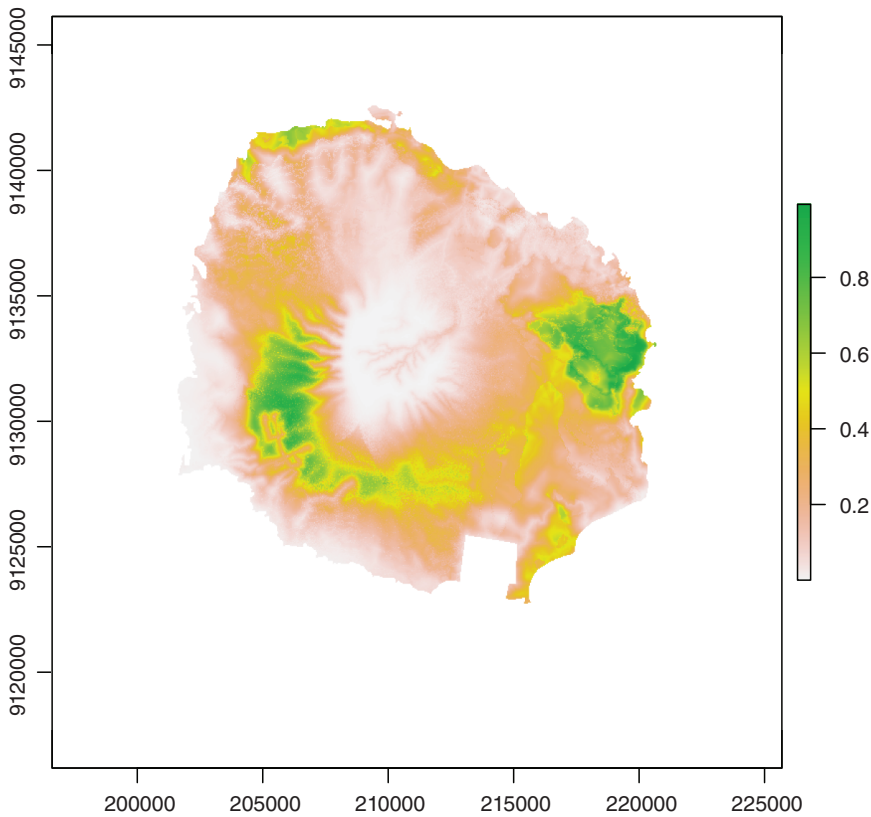ted density from the line transect survey, and the estimated abundance of 351,910 individuals larger than LTDS estimated abundance for the entire national park.

4 | DISCUSSION

When comparing the LTDS density estimate (41.4 ind/km^2) to the estimated density from the PDS survey (1,449 ind/km^2) there is a large difference. The nonrandom PDS provides seriously inflated density estimates (Marques et al., 2010). Yet, this method remains very common for assessing long-tailed macaque populations. Human provisioning seemed to attract long-tailed macaques to the roads and forest edges, and we conducted the nonrandom PDS to
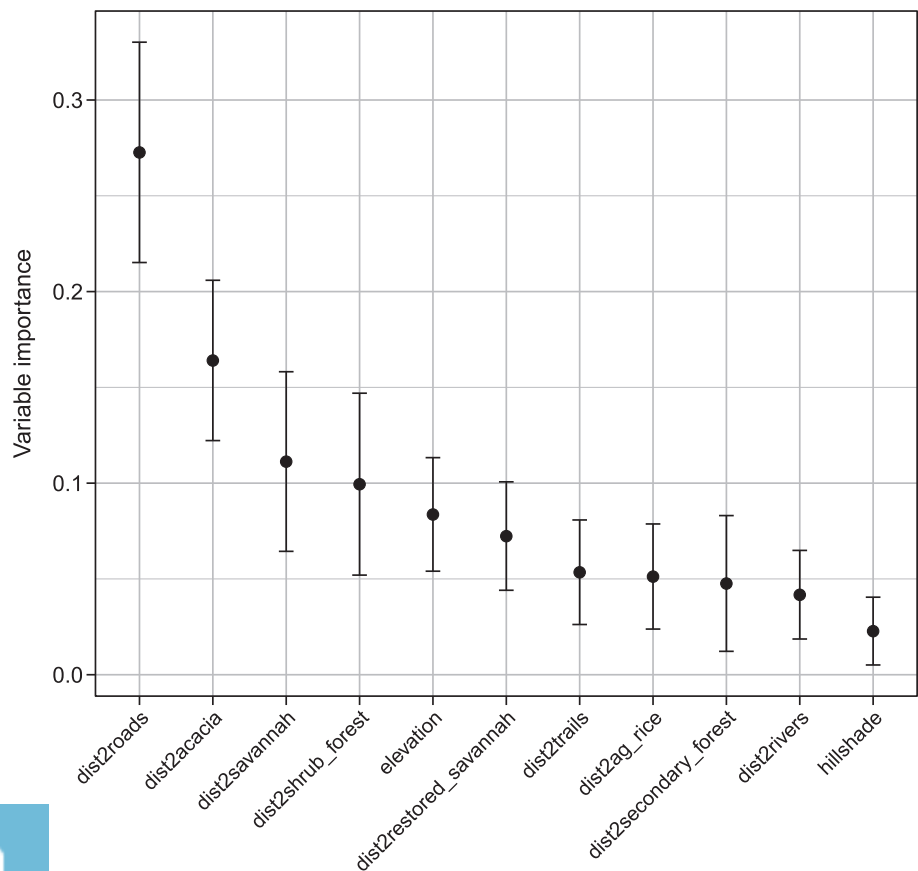
FIGURE 2 MaxEnt environmental variable importance in mean ΔAUC for distance to habitat variables as covariates

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FIGURE 3 MaxEnt habitat suitability map considering distance to habitat variables as covariates. The legend shows suitability ranging from high (green) to low (light red). The *x*- and *y*-axis is Universal Transverse Mercator (UTM) easting and northing

TABLE 3 Density and abundance estimates for nonrandom point distance sampling from Distance 7.1 for long-tailed macaques, uniform key, one cosine adjustment, 5% truncation, AIC

Parameter	Estimate	*SE*	%CV	*df*	95% CI
DS	102.77	16.70	16.25	24	73.64–143.43
E(S)	14.1	3.91	27.74	19	7.97–24.93
D	1,449	465.85	32.15	31	764.54–2,746.3
N (16.2 km^2)	23,474	7,546.8	32.15	31	12,385–44,491
N (250 km^2)	362,260	116,460	32.15	31	191,130–686,580

Note: AIC, Akaike Information Criterion; CI, confidence interval; CV, coefficient of variation; *D*, estimate of density of individuals (number per km^2); DS, estimate of density of groups (number per km^2); *df*, degrees of freedom; E(S), estimate of expected value (mean) of group size; *N*, abundance estimate.

highlight the consequences of assessing population density in anthropogenic areas and extrapolating this to other habitats, including nonanthropogenic habitats. In our case, this led to an overestimation of the population in BNP. Such overestimates were also the case in other areas in Java (Kyes et al., 2011). The opportunistic nature of long-tailed macaques make them highly adaptable, changing behavior, and group size according to habitat (Fuentes et al., 2008; Muroyama & Eudey, 2004), thus nonrandomized distance sampling is ill-suited for population assessments of this species, or any commensal species.

In 1995, Fooden reported a mean density of 55 ind/km^2 for nonprovisioned long-tailed macaque populations, and 100 ind/km^2 or above for provisioned populations across South East Asia based on a compilation of different surveys.

Our estimated LTDS density 41.4ind/km^2 in BNP was lower than Fooden's (1995) estimate for nonprovisioned groups. The exact methods used were unclear, and therefore strict conclusions should not be made when making comparisons. However, it could imply that the long-tailed macaque population density in BNP has not experienced a substantive population growth due to provisioning. The high visibility of long-tailed macaques in areas with provisioning may reflect a change in foraging and movement behavior instead of a change in population size. When comparing our LTDS results to provisioned groups in Bali (555-5850ind/km^2) (Brotcorne, 2014; Wheatley, 1989), again with caution to the difference in methods, our estimate was considerably lower (Table 1). In Vietnam provisioned groups had a mean density of 67ind/km^2 (Son, 2004), which is slightly higher

than our LTDS estimate (Table 1). In Singapore densities of 0.89–33.63ind/km^2 for semi-provisioned long-tailed macaques have been reported (Riley et al., 2015; Sha et al., 2009), and in Sumatran lowland forest nonprovisioned long-tailed macaques occurred at only 9.9ind/km^2 (Yanuar et al., 2009). Surveys from Java are few and dated, and our LTDS results can be used as a baseline for future population estimates in Java. Our results, if employed by BNP management can aid in creating informed long-tailed and tourist management decisions, especially our habitat suitability map can help prioritize focus areas and habitats.

Distance to habitats had the greatest importance for habitat suitability compared to percentage cover of habitats in our study. BNP is currently eradicating invasive acacia and trying to restore savannah habitats. Distance to restored savannah had little importance for long-tailed macaque habitat usage (Figure 2), and only the restored savannah areas with tourist sites were of preference (Figure 3). Restored savannah areas are still young (<5y), and may not have achieved the same biodiversity as native savannah. Distance to native savannah did have higher importance than distance to restored savannah, and we often encountered macaques in native savannah, where they foraged on grass seeds and other plants available, yet we did not encounter any in the large Merak savannah (Figure 3). This may be due to the presence of approximately 4,000 domestic cattle in the area that have changed the biodiversity and affected the presence of other animals (Pudyatmoko, 2017; Pudyatmoko et al., 2018). The presence of domestic cattle and settlements appear to have created a conflict of interest over food and water availability with the long-tailed macaques. For future conservation initiatives, the negative impact of domestic cattle presence should be taken into consideration. As mentioned, other areas in BNP are highly disturbed, such as the teak plantation, and this habitat did not prove suitable either (Figures 2 and 3). It is difficult to say if these habitats could be suitable if not heavily disturbed by human presence. In all other areas, except the Merak savannah, we did see long-tailed macaques, and with many seed dispersers having experienced a reduction in population size and/or change in distribution in BNP (Hakim et al., 2015; Hernowo, 1999; Semiadi & Meijaard, 2006), maintaining long-tailed macaques in nonanthropogenic areas may be of interest from an ecological point of view. The habitat suitability map shows preference for many different habitats at different levels, indicating that long-tailed macaques could employ several ecological roles in BNP.

Long-tailed macaques have previously been identified as edge species, only exploiting forest edges, habitats near rivers and other water sources, or human habitats on the edges of natural habitats (Fooden, 1995; Gumert et al., 2011). This, does not fit our findings completely. BNP experiences a long profound dry season, in which we still encountered long-

tailed macaques in habitats far away from water sources (Figure 3). These are not all highly preferred areas, like invasive acacia and native savannah, yet long-tailed macaques do use these areas (Figure 3). Distance to roads still had the highest variable importance of the habitat variables we tested (Figure 2). This indicates that resources were abundant at roads and trails and that this affected long-tailed macaque distribution.

BNP management has raised concerns on the provisioning of macaques, yet has not implemented any measures to mitigate this provisioning. If the goal is to reduce provisioning and mitigate human-macaque conflicts, our results clearly indicate that measures should be implemented on roads and trails, and in tourist areas (Figure 3). We recommend raising awareness amongst visitors and commuters regarding long-tailed macaque ecology, and also on the dangers of interacting with wildlife. We did not see any seasonality in human provisioning of macaques. Conducting the LTDS in other seasons and over several years, which we would have preferred would therefore not change the high variable importance of distance to roads. It could however, have reduced potential bias and provided knowledge on the seasonality in other habitats, as well as fluctuation over time.

Our survey design took seasonality into consideration for density and abundance results, and as such this should not have an effect on these estimates. For our habitat suitability analysis (Figure 3) however, we might have seen a slightly different map, and a different order of covariates in the variable importance graph. During the time of year, we conducted the survey, there were no water in the rivers in the park, and conducting the survey during high water availability would change the variable importance of rivers, as well as the habitats with fruiting trees, such as secondary forest.

Baluran Mountain was not included in our LTDS survey due to lack of accessibility. Anecdotal evidence suggests that long-tailed macaque density was extremely low on Baluran Mountain. Our estimate of 41.4ind/km^2 was probably higher than a true estimate including transects on Baluran Mountain. However, the natural flight distance of long-tailed macaques might also have affected our density and abundance estimates leading to underestimation. The effects of including both Baluran Mountain and correcting for natural flight distance are difficult to assess, yet mat not have been great due to the reciprocity of the two.

Kyes et al. (2011) conclude that we lack information about the Javanese long-tailed macaque population yet management plans keep being created and implemented, basing them on anecdotal evidence. Currently, a nationwide long-tailed macaque conflict mitigation task force in Indonesia under the Ministry of Forestry (BKSDA) is working on assessing human-macaque conflicts and finding solutions (R. M. Wiwied Widodo, personal communication, 2018).

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Recently, BKSDA issued a statement allowing the killing of long-tailed macaques in conflict zones in Java (Hardiyanto, 2018). However, with no reliable data on the population density and abundance of long-tailed macaques or the number of long-tailed macaques killed in conflict zones, for meat or pet trade, or harvested from the wild for medical research across southeast Asia, we do not know what the effects of culling may be. Our research shows that populations might be smaller than we think. Long-tailed macaques should be assessed across their range to ensure that population sizes are stable. Replicating systematic approaches covering entire study areas with points or transects randomly placed according to habitats and animal distribution in other long-tailed macaque habitats could improve knowledge base for this species and possibly lead to a reassessment of the conservation status of long-tailed macaques. We hope that employing the results from this study can assist in creating informed management decisions. Culling and relocation have been discussed in BNP, yet our results clearly show that BNP is not experiencing an overpopulation of long-tailed macaques. BNP is simply experiencing an increased density in more resource abundant areas—the anthropogenic areas, as is characteristic of this species across much of their range (Gumert et al., 2011).

Our study provides systematic data on a long-tailed macaque population with different levels of anthropogenic disturbance, and we hope policy makers and officials will take our results into consideration when looking at the conservation status of long-tailed macaques.

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CONFLICT OF INTEREST

We have no conflict of interests to declare.

AUTHOR CONTRIBUTIONS

M.F.H. has contributed to the conception and design, acquisition of data, analysis and interpretation of data, drafting of the manuscript, revision of the manuscript. V.A.N. has contributed to the acquisition of data and manuscript revision. F.M.B. has contributed to the analysis and interpretation of data, and manuscript drafting and revision. N.M.S. has contributed to the data analysis and interpretation and manuscript revision. C.T., A.F. and M.S. have contributed to the conception and design and manuscript revision. T.D. has contributed to the conception and design, interpretation of data and manuscript revision. All authors have given the final approval and are accountable for all aspects of the work.

DATA ACCESSIBILITY

Data is acceccible through DRYAD DOI: 10.5061/dryad.21kb2kq.

ETHICS STATEMENT

We have complied with ethics guidelines from University of Copenhagen Good Research and Publication Practice, the Indonesian Ministry of Research (RISTEK), Baluran National Park management, and Wiley Best Practice Guidelines on Publishing Ethics. The manuscript has not been published elsewhere. We did not handle any animals during this study and we conducted cut-as-we-go to minimize effect on vegetation.

ARTICLE IMPACT STATEMENT

Long-tailed macaque populations need to be reassessed using scientific rigorous methods to determine their population size and conservation status.

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SUPPORTING INFORMATION

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