Effect of Anthropogenic Activities on the Population of Moor Macaques (*Macaca maura*) in South Sulawesi, Indonesia

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Abstract

Forest loss due to anthropogenic activities is one of the main causes of plant and animal species decline. Studying the species' population status (i.e., density, abundance, and geographic distribution) on a regular basis is one of the main tools to assess the effect of anthropogenic activities on wildlife, to monitor population dynamics and to intervene with effective conservation strategies when the population of an endangered species declines. On Sulawesi Island, Indonesia, anthropogenic activities, such as agriculture, are decreasing the remaining natural habitats available for several endemic and endangered species. The effect of this forest loss on the threatened moor macaques (*Macaca maura*) in South Sulawesi is unknown, and data on the population status of this species are needed to design effective conservation strategies. To assess the population status of the moor macaques, we walked linear transects (N = 29, survey effort = 114 km) at six sites between November 2019 and March 2020 to estimate macaque population density and encounter rate. We tested the effect of anthropogenic activities on macaque encounter rate. Our global density estimate (24 individuals/km^2) was lower than the overall estimate from the most detailed survey conducted on this species, which covered its whole geographic distribution (36.1 individuals/km^2). However, these results should be interpreted with caution because the previous density estimate falls within the confidence intervals of our estimate. Furthermore, we found regional declines in moor macaque encounter rates in at least two sites compared with previous studies. We found a high presence of anthropogenic activity in the forests inhabited by macaques. Moor macaques were less abundant in open areas with no forest (i.e., clear cuttings) than in forested areas, and in the presence of nonspecies-specific hunting traps (i.e., wire-loop traps). Moreover, moor macaques were more abundant in areas with a higher presence of humans and domestic animals. Overall, our data suggest that the population of this

species may be declining in certain regions but further surveys are needed to corroborate whether this is occurring across the entire geographic distribution.

Introduction

Anthropogenic activities, such as agriculture, mining, and infrastructure development, are the main drivers of the modification and deterioration of natural environments (Sih, 2013; Díaz *et al.,* 2019). To date, almost 97% of the terrestrial surface of the planet has been altered by anthropogenic activities (Bersacola et al., 2021; Dirzo et al., 2014; Plumptre et al., 2021). Such activities affect species survival through natural resource exploitation and deforestation (Halpern et al., 2008; Parmesan and Yohe, 2003). For instance, agricultural areas are expanding in tropical regions, thereby replacing forests (Hansen et al., 2013; Phalan et al., 2013). In primate habitats, anthropogenic activities cause reductions in forest cover and resource availability, threatening primate populations (Boyle and Smith, 2010; Estrada *et al.,* 2017; Marsh & Chapman, 2013; Spaan *et al.,* 2020). This is especially the case in Southeast Asia, where at least 91% of the primate populations are declining (Amano et al., 2021; IUCN, 2019).

Species' population status (i.e., density, abundance, and geographic distribution) may vary along space and time as a result of habitat modification by anthropogenic activities (Estrada *et al.,* 2017; Wich & Marshall, 2016). Monitoring primate populations therefore provides important insights into how primates are adjusting to these modified habitats. Line transect surveys are the most commonly used method to survey primate populations (Buckland et al., 2010; Campbell *et al.,* 2016). During the past 50 years, data provided by line transect surveys have been used to monitor population dynamics and to take timely management decisions to protect declining populations of endangered species before it is too late (Caro *et al.,* 2012; Stokes *et al.,* 2010).

Sulawesi Island, Indonesia, lies at the centre of the Wallacea biodiversity hotspot and is inhabited by several endemic plant and animal species. For example, between 25% and 47% of all mammals, birds, amphibians, and reptiles living on the island are endemic (Lee *et al.,* 2007). However, many species inhabiting the island are endangered, because South Sulawesi is one of the most populated areas of Indonesia (the capital Makassar is the 4th largest city of Indonesia). Human population density in Sulawesi has quadrupled over the past 20 years (Supriatna *et al.,* 2020). The dramatic increase in human population, together with logging, hunting, mining, agricultural, and commercial development, constitutes a crucial threat to biodiversity conservation in Sulawesi (Kelley, 2018; Supriatna *et al.,* 2020). Moreover, deforestation has increased rapidly in recent years, in part due to the cultivation of corn, coffee, cocoa, and oil palm (Phalan et al., 2013; Supriatna *et al.,* 2020), forcing wildlife to live in relict patches of mature forest or in areas strongly affected by

anthropogenic activities (e.g., agriculture, logging, farming). To date, only 15% of Sulawesi forests are still intact, mostly steep, not-easily accessible areas where farming, logging, and other anthropogenic activities are difficult to be conducted and where resources for wildlife (i.e., food, water, and sleeping trees) are scarce (Supriatna *et al.,* 2015, 2020).

Sulawesi hosts seven species of the genus *Macaca*, which are all endemic (Riley, 2010). Of these, the moor macaque (*Macaca maura*) inhabits the Southern part of the island and is currently listed as Endangered by the IUCN Red List of Threatened Species (Lee *et al.,* 2020). Moor macaques live in groups of around 40 individuals, with female philopatry and male dispersal (Okamoto *et al.,* 2000). The last study estimating the density (i.e., number of individuals/area) and structure of the moor macaque population was published more than 20 years ago (Okamoto *et al.,* 2000) and only surveyed a small part of the species' geographic range (i.e., the Karaenta Natural Reserve). In this area, group size grew continuously during the 10 years of the study, from 20 to 41 individuals, with a population density of 70 individuals/ km^2 (Okamoto *et al.,* 2000). A more recent report, published in Bahasa Indonesian, surveyed one single regency (Pangkep, South Sulawesi) located in the Western part of their geographic range and estimated a population density of 98 individuals/km^2 (Labahi, 2010).

To our knowledge, the only survey that has estimated population density across the entire known geographic range of moor macaques was conducted 33-35 years ago, between December 1987 and October 1989 (Supriatna *et al.,* 1992). This study estimated that the population of moor macaques was decreasing strongly (Supriatna *et al.,* 1992). Moreover, groups of moor macaques inhabiting areas with intense anthropogenic activity (e.g., logging or farming) were smaller, had a lower ratio of infants and juveniles to adults, and a population density less than half that of groups in protected areas (20 vs. 50 individuals/km^2, respectively; Supriatna *et al.,* 1992). Finally, the moor macaque population appeared to be mainly threatened by the lack of protected areas in the species' range and by the increasing impact of anthropogenic activities on macaques in all the areas surveyed, including illegal poaching and poisoning (Supriatna *et al.,* 1992). Moor macaques have been mainly found in resource abundant lowland forests (Albani *et al.,* 2020; Li & Rogers, 2005) and, at lower densities, in karst areas (Lee *et al.,* 2020). In the last decade, however, the moor macaque geographical range has become largely restricted to karst areas (Albani *et al.,* 2020; Supriatna *et al.,* 2020), likely because these areas are less accessible and thus less impacted by anthropogenic activities.

In response to the decline in the moor macaque population, the Indonesian authorities created the Bantimurung-Bulusaraung National Park in 2004. Although moor macaques are being studied in the National Park (Albani *et al.,* 2020; Hanson and Riley, 2018; Morrow *et al.,* 2019; Okamoto *et al.,* 2000; Riley *et al.,* 2014), it is not clear to what extent the National Park is preventing the decline of the macaque population (Lee *et al.,* 2020), as the park also is affected by the increase in anthropogenic activities occurring throughout Southern Sulawesi. For example, the second busiest road crossing South Sulawesi traverses the National Park.

The lack of recent data on the moor macaque population size makes it difficult to reliably estimate its conservation status and evaluate whether current conservation

strategies are effective (Junker *et al.,* 2020; Lee *et al.,* 2020). Monitoring the population density of moor macaques, both in and outside protected areas, is essential to identify macaque-rich areas that should be protected (Ahmed *et al.,* 2021; Gray *et al.,* 2016; Lee *et al.,* 2020; Milda *et al.,* 2020). We surveyed six sites across South Sulawesi to provide updated estimates of (a) the size of the moor macaque population and (b) the effect of anthropogenic activities on the regional relative abundance of macaques (i.e., the number of individuals/km surveyed). If populations are declining due to anthropogenic activities, we predict that (1) overall and regional macaque population density would be lower than previous estimates; and (2) the relative abundance of moor macaques would be negatively correlated with anthropogenic activities, estimated by, e.g., the presence of humans, of domestic animals, or of traps.

Methods

Study Site

We surveyed the Southern part of the geographic range of moor macaques, from Bontobahari (5°33'1.33"S, 120°24'45.78"E) to Camba (4°59'36.60"S, 119°45'7.13"E; Fig. 1). The areas surveyed lie between zero and 2,874 m.a.s.l. and are composed of a mosaic of deciduous forest interspersed with grasslands (resulting from habitat conversion), primary and secondary forests surrounded by agricultural areas, karst forests, and savannah (Lee *et al.,* 2020).

Data Collection

We selected areas to be surveyed within the geographic range of moor macaques described by the IUCN (Lee *et al.,* 2020; Supriatna *et al.,* 2008). We selected areas based on: 1) the presence of suitable habitats for the macaques; and 2) informal interviews with the local community (i.e., people living close to the forest or working in the forest, and local authorities) about the presence/absence of macaques in the area. Since 2018, we have collected information about the presence of moor macaques in different habitat types within its geographical distribution (unpublished data) during the data collection for other research projects in Sulawesi (Amici *et al.,* 2020; Beltrán Francés *et al.,* 2020; Gomez-Melara *et al.,* 2021; Hernández Tienda *et al.,* 2021). Therefore, we used this information to select suitable habitats to survey the moor macaque population (Kuhl *et al.,* 2008).

We considered a habitat as suitable for macaques when forest cover was ≥50% per km^2, because this is necessary for moor macaques to find shelter and food (Fotang *et al.,* 2021). We considered primary, old and young secondary forest and agroforest (i.e., forest area composed of natural plant species growing among crops; Nekaris *et al.,* 2017) as suitable forest types for moor macaques. We did not consider production forests (i.e., consisting of nonnative tree species, such as rubber production forest) as a suitable habitat. We determined forest cover every 10 km^2 in
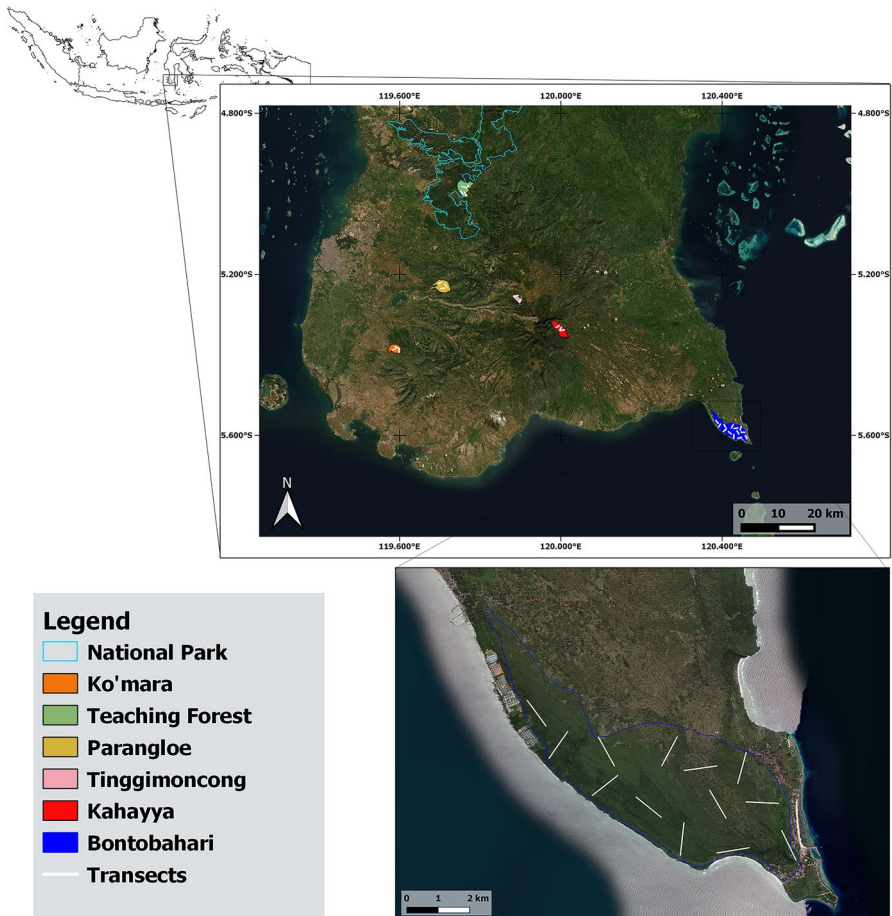
Fig. 1 Map of South Sulawesi showing the location of 6 areas surveyed in the *Macaca maura* geographic range and of the transects walked in Bontobahari between November 2019 and March 2020.

the overall study area, using satellite images from 2019 (Landsat) in Google Earth Pro (v.7.3.3).

To conduct informal interviews with local communities, we first informed local authorities at each study site about the aims of our project and the importance of conducting interviews with the communities to gather information on the distribution of moor macaques. After obtaining verbal informed consent from the local authorities and the interviewees, we conducted the interviews outside the interviewee's house at least 1 week before surveying the area. We conducted all interviews in the presence of local authorities.

We conducted line transect surveys to estimate the presence/absence of moor macaques and their population size and composition (Butynski, 1990; Harcourt, 1995; Plumptre & Reynolds, 1994; Worman & Chapman, 2006). We positioned twenty-nine, 1 km-long transects pseudo-randomly on the satellite image of the

selected areas (Google Earth Pro, v.7.3.3), trying to cover each area as much as possible. We covered 12% of the overall selected area (effort = 9.12 km², Table I). We calculated the overall area covered during surveys by multiplying the number of transects by the area covered by each transect (i.e., effort: length of the transect times the width of the area checked at both sides of the transect), divided by the total size of the areas surveyed. The satellite image included altitude contour lines (every 50 m) providing information on the topography of the terrain. We distributed transects randomly on the map and relocated transects that were less than 1 km from another transect or outside of suitable areas, by moving them to an empty area while maintaining the same orientation. We also reoriented transects that were located over rivers or areas with steep slopes. We ground-truthed the location of transects once we were in each location to make sure that the slope and vegetation of the area matched what was predicted by the satellite images. We established 1 km as the minimum distance between transects based on the size of the area being surveyed and the expected density and home range of the macaques (Okamoto *et al.,* 2000; Supriatna *et al.,* 1992). The distance between transects in each surveyed area ranged from 1 km to 1.81 km, with a mean distance of 1.23 km.

The first author collected the data between November 28, 2019 and March 20, 2020. We walked each transect twice on two consecutive days, between 9:00 and 15:00, at a maximum speed of 1 km/hr. While walking the transects, the first author used a GPS unit (Locus Map 4.1; Asamm Software 2009) to keep line transects correctly orientated from start to end. When transects included steep inclines, declines, and gorges, we used marked stakes to make accurate distance and orientation measurements (Alldredge *et al.,* 2007). During the survey, we recorded GPS coordinates every time that we detected a macaque. To test whether macaques were found above 1,000 m a.s.l, we used the GPS coordinates to estimate the elevation of all sightings recorded using Google Earth Pro (v.7.3.3). Whenever possible, we recorded the sex (in adults) and age category (using two categories: adult and immature, which included subadults, juveniles, and infants) of each individual detected. We determined sex and age category by observing the genitalia (i.e., individuals with evident genitalia: testicles for males, anogenital swelling for females) and body size (Okamoto *et al.,* 2000). When a female macaque did not present an anogenital swelling, we used body size to determine age, as immatures are smaller than adults in this species (Okamoto *et al.,* 2000). We took a picture of each individual observed to check sex and age after data collection, where necessary. If we did not observe a macaque directly above or on the transect (i.e., perpendicular distance = 0), we used a Laser View Finder (Urceri ZL-100) to measure the perpendicular distance from the transect centreline to the individual. Because there are no published data on group spread in our study species, we considered multiple sightings of macaques along the same transect as belonging to the same group, based on the mean group spread of a closely related species, Celebes crested macaque (*Macaca nigra* 1,128 m²; Waterman, 2021).

To test the effect of anthropogenic activities on the moor macaque population, we recorded the presence and type of anthropogenic activity observed during surveys (Fig. 2). We measured anthropogenic activities as nonmutually exclusive categories: (1) number of humans (e.g., farmers or loggers) detected during the transect walk,

Table I Regions where we collected data during the population survey, area covered during transect walks and population density estimates per region for *Macaca maura* from November 2019 to March 2020 (South Sulawesi, Indonesia)

| Region	Area (km²)	Forest cover (km²)	Transects (N)	Effort (km²)	Groups (N)	Macaques (N)	Group encounter rate (groups/km)	Individual encounter rate (individual/ km)	Density (individuals/ km²)	Confidence intervals
Bontobahari	28.30	26.90	13	4.15	7	57	0.27	2.20 (3.39*)	27.4 (33.9*)	13.7–55.0
Camba	12.70	12.10	4	1.27	2	13	0.25	1.63		
Kahayya	9.45	7.95	4	1.24	2	12	0.26	1.55		
Tinggimoncog	3.60	3.40	2	0.59	0	0	0.0	0.0 (0.0*)		
Parangloe	12.70	10.80	3	0.96	1	8	0.16	1.33		
Ko'mara	6.76	5.66	3	0.91	3	17	0.53	2.98		
Overall	73.51	66.81	29	9.12	15	107	0.26	1.88 (3.83*)	24.0 (36.1*)	14.6–39.4

*Data from Supriatna *et al.*, 1992
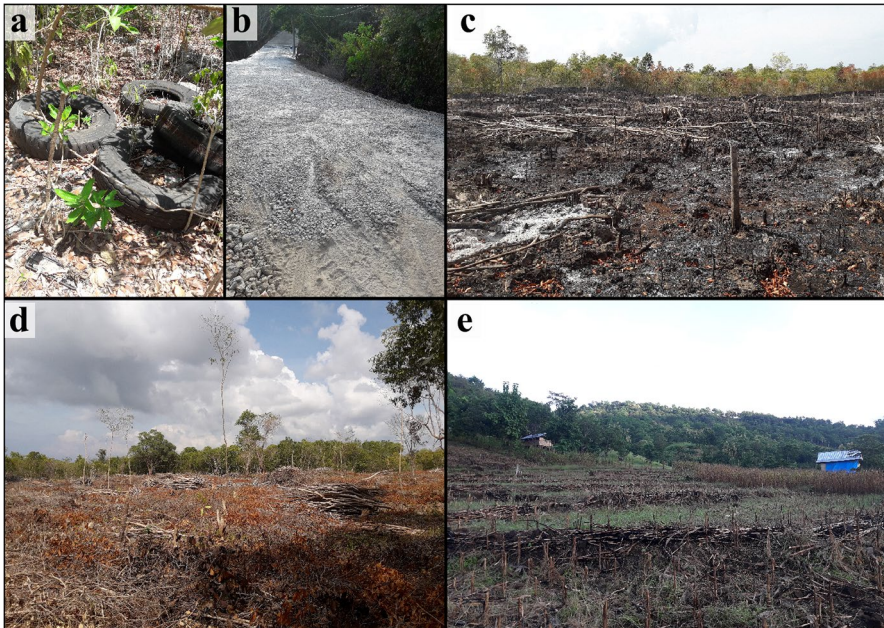
Fig. 2 Examples of anthropogenic activities recorded during data collection in the geographic range of *Macaca maura*, South Sulawesi, between November 2019 and March 2020: **a** garbage; **b** road; **c** fire; **d** logging; **e** agricultural plots.

(2) number of domestic animals (i.e., cows, goats, sheep or dogs) detected during the transect walk, (3) number of hunting traps (i.e., nonspecies-specific snare traps used to hunt other species but that might accidentally trap macaques) detected during the transect walk, (4) open areas with no forest (i.e., agricultural plots, clear cutting, or logging, in m^2), and (5) areas with other anthropogenic activities (i.e., camp, fire, garbage/waste disposal, or construction, in m^2). The use of snare traps is banned in Indonesia, but this hunting practice is still used in some areas. When we encountered any of these types of anthropogenic activity along the transect, we recorded the GPS location. When we encountered open areas or areas with other anthropogenic activities, we recorded the perpendicular distance from the transect centreline to the nearest forest patch using the Laser View Finder and the distance walked through the anthropogenic activity area (marking the beginning and the end of the area with a GPS). We used these distances to estimate the size of open areas and areas with other anthropogenic activity during the transect walk in km^2 (Fig. 1).

Data Analysis

We estimated moor macaque population density using the conventional distance sampling (CDS) method for line transect surveys (Buckland *et al.,* 2001, 2015) in Distance software (Thomas *et al.,* 2010). CDS assumes that all the animals on the

transect are detected and that detection probability decreases with distance from the transect (Buckland *et al.,* 2001, 2015; Spaan *et al.,* 2019). Distance software uses the perpendicular distances (*x*) to model the detection function *g(x)*. *g(x)* is defined as the probability of detecting a macaque that is at distance *x*, where $0 \leq x \leq w$ and *w* is the truncation distance (i.e., maximum perpendicular distance from the transect centreline beyond which detected individuals are excluded from the density estimation). To select a plausible and parsimonious model estimating *g(x)*, we tested three key functions (i.e., uniform, half-normal, and hazard-rate) with three adjustment terms (i.e., cosine, simple polynomial, and hermite polynomial; Buckland *et al.,* 2001, 2015; Spaan *et al.,* 2019). We compared the models obtained using the Akaike information criterion (AIC) and chose the best fitting model(s) that differed less than 2 units from the lowest AIC (i.e., Delta AIC < 2) and had the fewest parameters (Buckland *et al.,* 2001). To improve the robustness of the perpendicular distance data analysis, we right-truncated *w* to 5%, discarding the largest distances from the analysis (Buckland *et al.,* 2001; Marques et al., 2011; Valente et al., 2016; Spaan *et al.,* 2019). We calculated the overall population density based on all sites and for sites with observations of at least 40 individual macaques (Buckland *et al.,* 2001; Marshall *et al.,* 2008). Finally, for a more detailed assessment of whether the population of moor macaques is declining, we compared the relative abundance (encounter rates) of macaques at each site that was also surveyed in the previous survey (Supriatna *et al.,* 1992). For this comparison, we used individual encounter rates (number of individuals encountered per kilometer walked) for each site and transect (Chapman *et al.,* 2018; Spaan *et al.,* 2020). To calculate individual encounter rates from the previous study (because these data were not available), we estimated the distance walked in each site by Supriatna *et al.* (1992) by dividing the area surveyed by the width of the transects (100 m; Southwick & Cadigan, 1972; Struhsaker & Eisenberg, 1981; Wilson & Wilson, 1975).

We tested the effect of anthropogenic activity on moor macaque encounter rate by using a generalized linear mixed model (GLMM) with a Poisson distribution and log link using the glmmTMB package (version 1.0.1; Brooks *et al.,* 2017) in R (R Development Core Team, 2013, version 3.5.2). We entered the individual encounter rate per transect into our model as a dependent variable. We entered the length of the transect as an offset term. We included the following test predictors: (1) number of humans, (2) number of domestic animals, (3) number of nonspecies-specific traps, (4) open areas, and (5) other anthropogenic activities. We defined a single transect as the unit of analysis. Finally, because we walked each transect twice, we entered transect identity as a random factor (Bolker *et al.,* 2009). We *z*-transformed continuous predictor variables before running the analyses to improve normality and facilitate interpretation of the results (Kirkpatrick *et al.,* 2017). We used likelihood ratio tests to compare the full model, containing all predictor variables, to a null model containing only the random factor and the offset term (Forstmeier & Schielzeth, 2011). If we found a significant difference between the full and the null model, we conducted likelihood ratio tests to obtain the *P* values for each test predictor via single-term deletion, using the R function drop. We detected no stability, convergence, and dispersion problems with the GLMM, using the DHARMa

package (Hartig, 2021). Variance Inflation Factors (VIFs) were minimal for all test predictors (maximum VIF = 1.95), indicating low collinearity (Field, 2005).

Ethics Note

Permission to conduct the informal interviews and the population survey was granted by the RISTEKDIKTI (Indonesian Foreign Research Permit Division, Ministry of Research and Technology/National Research and Innovation Agency). RISTEKDIKTI also granted access to the moor macaques. This study followed the Code of Best Practices for Field Primatology, from the International Primatological Society (2014). The authors have no conflict of interest to declare.

Data Availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Results

We selected six areas to survey (Fig. 1), which were mostly covered by forests (91% of surveyed areas; Table I). During the 57 km of transects surveyed (n = 29; Table I), we sighted 107 moor macaques belonging to 15 groups (Table I; Fig. 1). Overall macaque encounter rate was 1.88 individuals per kilometer walked, with the highest encounter rate in Ko'mara (2.98 individuals/km) and the lowest in Tinggi-moncong (0 individuals/km; Table I). We encountered macaques on 52% of the transects (15/29), and during both transect walks in only 17% of the transects (5/29). We observed moor macaques at elevations between 18 and 1316 m a.s.l. (mean: 287 ± SD: 372 m). Both individual and group encounter rates were higher in areas under 1,000 m a.s.l. (2.08 individuals/km; 0.29 groups/km) than above 1,000 m a.s.l. (1.05 individuals/km; 0.18 groups/km), but this difference was not statistically significant (individuals: ANOVA: F = 3.043, df = 1, $P = 0.156$; groups: ANOVA: F = 1.447, df = 1, $P = 0.295$). We determined the sex and age category for 34 monkeys (32%): 16 adult males, 8 adult females, and 12 immatures of unspecified sex.

As the probability of detecting a macaque decreased with distance from the transect centerline, the detection function that best fit the perpendicular distance data was the half-normal key function with a simple polynomial adjustment term. We discarded two perpendicular distances (62 m and 64 m) from the analysis after right-truncating the largest distances. We estimated the overall population density as 24.0 individuals/km^2 (Table I).

We found signs of anthropogenic activity on all 29 transects. "Other anthropogenic activities" was the most frequent activity observed (97%). Agriculture was more abundant in Northern areas (Tinggimoncong, Ko'mara and Kahayya; 75% of the transects) than in the Southern area (Bontobahari; 30% of the transects), where the weather is drier and agricultural fields are therefore less common. We found domestic animals on 62% of the transects (18/29 transects) and hunting traps on 5

transects, all in the Southern area (38% of transects in Bontobahari). The number of traps per transect ranged from 0 to 3.

The full GLMM model differed significantly from the null model (likelihood ratio test: $\chi^2 = 16.883$, df = 5, $P = 0.005$). As predicted, the individual encounter rate was lower in areas with more open spaces and with no trees than in areas with greater forest cover (Table II). Moreover, the individual encounter rate was lower when more traps were found in an area and higher when more domestic animals were sighted in the area (Table II). The other test predictors had no significant effect on individual encounter rate (Table II).

Discussion

Our findings suggest that the population density of moor macaques is low outside of protected areas and support our hypothesis that the population of this species is declining in several regions, especially in the Southern forests of the species' geographic range. Specifically, we found a lower macaque encounter rate in 2020 than at the same sites surveyed in 1992. Furthermore, we found a high presence of anthropogenic activity in forests inhabited by moor macaques, and a negative effect of the number of nonspecies-specific hunting traps in the forest on macaque encounter rate.

We calculated the overall population density and the individual encounter rate, from the data provided in the previous study of moor macaque populations, as 36.1 individuals/km^2 and 3.83 groups/km (Supriatna *et al.,* 1992). Although direct comparisons between studies are difficult, due to differences in the sites surveyed and the methods used to estimate population density, our overall density estimate (24 individuals/km^2) and encounter rate (0.94 individuals/km) were lower, but the density estimate from 1992 (Supriatna *et al.,* 1992) falls within the confidence intervals of our estimate. Therefore, these differences should be interpreted with caution and further surveys are needed to verify whether the overall moor macaque population density is decreasing. Moreover, surveys in the Northern region of the species' geographical distribution are urgently needed to understand the current state of populations there.

Table II Results of a GLMM model testing the effect of anthropogenic activities on the population size of *Macaca maura* from November 2019 to March 2020 (South Sulawesi, Indonesia)

	Estimate	SE	2.5% CI	97.5% CI	z	LRT	df	P
Intercept	−7.84	0.567	−8.951	−6.728	−13.825	-	-	**-**
Presence of humans	0.61	0.3234	−0.028	1.240	1.874	3.612	1	0.057
Presence of domestic animals	0.93	0.387	0.171	1.689	2.401	6.732	1	**0.009**
Presence of traps	−1.42	0.872	−3.128	0.290	−1.627	5.353	1	**0.021**
Open areas	−0.96	0.466	−1.874	−0.048	−2.063	5.148	1	**0.023**
Other anthropogenic activity	−1.02	1.115	−3.208	1.163	−0.917	2.633	1	0.105

In bold are *p* values <0.05

In the Southern part of Sulawesi (Bontobahari), macaque encounter rate was relatively high in 1992 (3.39 individuals/km) but decreased to 2.20 individuals/km during our survey. Worryingly, although this area falls under local protection (i.e., logging and hunting are forbidden by the local government and communities), forest loss is still occurring due to the expanding tourism industry and agriculture (Supriatna *et al.,* 2020). Furthermore, the long dry season in this Southern area (7 dry months per year on average; Supriatna *et al.,* 1992) may further increase the negative effects of anthropogenic activities on the moor macaque population (Campos *et al.,* 2017; Garber *et al.,* 2020; van Schaik & Brockman, 2005). For instance, sleeping sites are scarce in the area due to logging for the traditional boat building industry (Supriatna *et al.,* 1992), and forest recovery after logging may be strongly hindered by dry climatic conditions (Elias *et al.,* 2020; Graham *et al.,* 2016; Lewis *et al.,* 2015; Stewart *et al.,* 2020).

We observed a similar decrease in moor macaque encounter rate in the National Park in the district of Camba. In mixed primary and secondary forests, we estimated macaque encounter rate at 1.63 individuals/km. Encounter rate in the closest location monitored in 1992 (Karaenta, 7 km from Camba, located in the same National Park) was estimated at 5.19 individuals/km. Although the forest of Camba is protected by Bantimurung-Bulusaraung National Park, human settlements and road traffic are abundant (Supriatna *et al.,* 1992; Zak and Riley, 2017), putting macaques at risk of road accidents and food-provisioning, which can have deleterious health effects (Healey *et al.,* 2020; Riley *et al.,* 2021). Despite the implementation of protective measures in this region of Southern Sulawesi, ongoing anthropogenic activities are still likely to threaten the long-term maintenance of moor macaque populations.

One of the main anthropogenic activities in Sulawesi outside protected areas is agriculture (Supriatna *et al.,* 2020). As a result, primates are often found in areas where agricultural fields and forests are mixed (Campbell-Smith *et al.,* 2011; Estrada *et al.,* 2012). We conducted macaque surveys in agroforests (e.g., corn and coffee plantations interspersed or surrounded by forest) and found that moor macaque encounter rate was lower during our survey than in 1992. For instance, moor macaque encounter rate in agroforests in Ko'mara was estimated at 2.98 individuals/km, the highest value among our survey regions, but still far from the 6.34 individuals/km estimated in similar agroforests 32 years ago (Supriatna *et al.,* 1992). During our surveys, we observed macaques inhabiting agroforests in Ko'mara feeding on corn plantations. Moor macaques prefer corn and fruit crops to coffee, cacao, or rice (Supriatna *et al.,* 1992; Zak and Riley, 2017). It is therefore possible that the type of crop explains the high encounter rate of macaques estimated in Ko'mara, an area mainly covered by corn plantations. In addition, some of the local people that we interviewed in Ko'mara mentioned that several macaque groups use agricultural fields to move between forest patches. Thus, the combination of small-scale agricultural plots with well-conserved forest, at the landscape scale, may have a positive effect on moor macaque populations (Kiffner *et al.,* 2020). This is in line with studies showing that agroforests can support populations of several primate species (Campbell-Smith *et al.,* 2010; Estrada *et al.,* 2012; Riley, 2010). A better understanding of the effect of agroforests on the abundance and distribution of moor macaques is therefore crucial to develop effective conservation strategies that benefit

local farmers and macaques. We suggest that such studies should be performed at the landscape scale (Arroyo-Rodríguez & Fahrig, 2014; Galán-Acedo *et al.,* 2019; Junker *et al.,* 2020) to determine the importance of the remaining forest cover for the use of agroforests by macaques.

Anthropogenic activities are concentrated in lowland areas of Sulawesi, and as a result, moor macaque populations are likely displaced to remnant forest patches at higher altitudes (i.e., mountains and karst towers; Albani *e*t al., 2020; Supriatna *et al.,* 2020). To date, moor macaques have been found from 0 to 2,000 m a.s.l. (Lee *et al.,* 2020). In our study, encounter rate was higher at lower altitudes (e.g., Ko'mara, 300 m a.s.l.; Table I) than in similar habitats located at elevations beyond 1,000 m a.s.l. (e.g., in Kahaya, at 1,200 m a.s.l.), although the difference was not significant. Further data are needed to determine whether groups of macaques inhabiting highland areas, where resources are scarce compared with lowland areas (Supriatna *et al.,* 2020), are smaller (Albani *et al.,* 2020; Lee *e*t al., 2020). If this hypothesis is confirmed, groups of moor macaques that have been forced to live in the mountains due to anthropogenic activities may face greater ecological challenges and be at greater risk of extinction. We did not observe any macaques in Tinggimoncong, a mountainous area (1,500 m a.s.l.) composed of a mix of young and old secondary forest, pine forest, and agriculture fields (e.g., vegetables, coffee, and corn). This result is in line with the data reported in the last survey in the region, where no macaques were observed either (Supriatna *et al.,* 1992). The high location of the region and the increase in agricultural fields in the area (Supriatna *et al.,* 2020) may explain the continued scarcity of macaques in Tinngimoncong.

As a result of a rapid reduction in forest cover over the past 30 years (Phalan, 2013; Supriatna *et al.,* 2020), some of the surveyed areas are separated by ≥40 km and are not connected by ecological corridors. The southernmost forest patch we surveyed (Bontobahari), for instance, is isolated from other forests by agricultural fields and human settlements, limiting macaque dispersal or causing them to take potentially deadly risks, such as crossing highly trafficked roads. The lack of ecological corridors connecting the different areas inhabited by moor macaques implies that their populations are likely fragmented, limiting gene flow and potentially affecting long-term population viability (Fa & Tagg, 2016; Meijaard & Nijman, 2000). Furthermore, moor macaque encounter rate was positively associated with forest cover, and macaques were seldomly observed in open areas. Therefore, conservation efforts should focus on protecting the remaining forests of South Sulawesi from forest conversion to other land covers (Malik *et al.,* 2015; Supriatna *et al.,* 2020; Waluyo *et al.,* 2005; Whitten & Henderson, 2012) to maintain connectivity between remnant subpopulations.

We found that the number of macaques was significantly lower in areas where snare hunting-traps were more abundant. Although these traps are mostly used by local people to hunt other species of mammals (e.g., wild pigs; personal observation; Latinne *et al.,* 2020), the use of nonspecies-specific traps may affect the population of protected and threatened species, including moor macaques (Borgerson, 2015; Rosenbaum *et al.,* 1998; Waller & Reynolds, 2001). This result is in line with studies of other species. For instance, the use of snare traps to hunt tigers (*Panthera tigris*) in Sumatran forests led to a decrease in the population of Malayan tapir (*Tapirus indicus*; Campbell *et al.,* 2019). Populations of terrestrial primate species have

also been negatively affected by the presence of snare traps in their habitats (Fa & Yuste, 2001; Kumar & Sankhyan, 2021; Munn, 2006; Quiatt *et al.,* 2002; Yersin *et al.,* 2017). For example, chimpanzee (*Pan troglodytes*) populations inhabiting areas where snare traps are present show lower survival rates due to the wounds inflicted by these traps (Munn, 2006; Yersin *et al.,* 2017). Deforested areas may induce more terrestrial habits in the primate species occurring there, increasing the negative effects of snare traps on primate populations (Figel *et al.,* 2021). The high rate of deforestation in South Sulawesi (Supriatna *et al.,* 2020), together with the presence of snare traps in areas where they occur, may therefore negatively affect the survival of moor macaques. The consistent enforcement of banned, nonspecific hunting techniques, together with the implementation of long-term and local conservation projects, may reduce this threat to macaques and other terrestrial species (Gray *et al.,* 2018)

We found that macaque encounter rate was higher in areas with a higher number of domestic animals, which can be considered a proxy of the intensity of anthropogenic activity in an area. There are three plausible explanations for these unexpected results. First, it is possible that macaques prefer to use relatively flat areas (compared with karst areas), which also are usually preferred by farmers and shepherds for their crops and herds (Albani *et al.,* 2020; Anderson & Mammides, 2020; Estrada *et al.,* 2017; Mwenja, 2007). Second, these results may suggest that macaques often are found near human settlements because of increased anthropogenic activity and habitat loss (Estrada *et al.,* 2012, 2017). For instance, macaques living in human-modified habitats may find resources (e.g., food and water) in areas close to human settlements in the form of crop fields or water tanks (Sha *et al.,* 2009). Finally, shepherds might be using the forests close to their settlements to feed their cattle, increasing competition for available food resources (Wich & Marshall, 2016). This scenario increases the risk of human-macaque conflict and persecution due to crop foraging (Riley & Priston, 2010) and represents a significant threat for the persistence of moor macaque populations. Furthermore, increasing interactions between wildlife and domestic animals enhance opportunities for pathogen transmission (Jori *et al.,* 2021), especially in human-modified habitats (Jones *et al.,* 2013). For instance, several Asian endemic pig species are threatened by a virus transmitted by domestic pigs (*Sus scrofa*; Luskin *et al.,* 2021) and endangered species, such as the African wild dog (*Lycaon pictus*) or the Ethiopian wolf (*Canis simensis*), face disease outbreaks due to interactions with free-ranging livestock in their habitats (Higgitt *et al.,* 2019; Johnson *et al.,* 2014). Coexistence between wildlife and domestic animals therefore should be monitored by conservation authorities (Kiffner *et al.,* 2020).

Sulawesi Island lies at the centre of the Wallacea biodiversity hotspot, one of the world's 36 biodiversity hotspots (https://www.conservation.org/priorities/biodiversity-hotspots), and the forests inhabited by moor macaques also host many other endemic and endangered species (Brambach *et al.,* 2017; Evans *et al.,* 2003). If deforestation continues at current rates, moor macaque habitat will be increasingly threatened, potentially leading to local population extinctions (Supriatna *et al.,* 1992, 2020). Urgent conservation measures are therefore needed to conserve the forests of Sulawesi and the species that inhabit them (Estrada *et al.,* 2018; Supriatna *et al.,* 2020). Conservation measures should include extended protection of moor macaque habitat (with corridors connecting isolated areas), projects encouraging ecologically

sustainable activities in communities living alongside macaque populations to avoid potential conflict over resources, and environmental education projects aimed at raising awareness of the ecological importance of moor macaques and the threats faced by their populations. Special attention should be paid to isolated patches of forest surrounding the National Park, such as Bontobahari forest, which could be connected to the Southern part of the National Park through the implementation of forest corridors and reforestation projects. Moreover, a complete population survey focusing on the impact of different anthropogenic activities on the density, distribution, and demography of the moor macaques at a landscape scale is urgently needed (Lee *et al.,* 2020; Supriatna, 2019). As the geographic range of the species covers the complete region of South Sulawesi (Lee *et al.,* 2020), surveys should aim to identify remaining suitable habitat across the region and priority areas for their conservation.

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