



# Activity budget, home range, and habitat use of moor macaques (*Macaca maura*) in the karst forest of South Sulawesi, Indonesia

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## Abstract

Primate behavior can be responsive to the different ecological pressures associated with different habitats, as well as to the effects of direct and indirect anthropogenic disturbance. The karst forest ecosystem of South Sulawesi (Indonesia) represents one of the few intact forests available for residual populations of the moor macaque, but our understanding of its habitat use is limited. In the present study, this gap in knowledge was addressed by observing the activity and habitat use of two groups of moor macaques and by assessing the suitability of different habitats in the karst forest. Through a fine-scale vegetation analysis of 1 ha of forest in Bantimurung Bulusaraung National Park, we identified the presence of two distinct habitats that differ in terms of forest structure and composition. The karst plain forest (KPF) provided a greater abundance and diversity of food resources than the karst tower forest (KTF). In addition, anthropogenic disturbance was high in the KPF but low in the KTF. Behavioral data collected via group scans indicate that the macaques devoted more time to feeding activities when in the KPF, suggesting an ability to adjust their feeding behavior to meet their nutritional needs. However, the larger of the two groups used the food-rich KPF more than expected, implying that the KTF may represent a valuable refuge for the smaller group, as it is a less risky portion of its home range. The results of this study therefore provide novel information on the ecology of moor macaques and their habitats that can inform conservation planning for remnant populations.

**Keywords** Sulawesi macaques · Forest structure and composition · Feeding ecology · Anthropogenic disturbance · Conservation

## Introduction

Habitat structure and composition are known to be two of the main determinants of primate diversity and abundance in tropical forests (e.g., Pyritz et al. 2010). Ecological variables such as forest productivity, precipitation, and seasonality influence primate density and diversity at the landscape level

(e.g., Pinto et al. 2009), while differences in forest structure and composition may make different habitats available to primate species at the local level (e.g., Bobadilla and Ferrari 2000). For many primate species in tropical regions, however, these habitats are being threatened by habitat fragmentation resulting (either directly or indirectly) from encroaching human populations and their activities (e.g., Cowlshaw 1999; Harcourt and Parks 2003).

The survival of many forest-dwelling nonhuman primates (“primates” hereafter) largely depends on their ability to cope with reduced habitat patches (Fahrig 2003) or increased isolation (Marsh 2003). As forest structure and composition can be severely altered by fragmentation (Arroyo-Rodríguez and Mandujano 2006), species’ response patterns to fragmentation are expected to vary considerably according to habitat and forest type (Huang et al. 2017). In heterogeneous ecosystems, the distribution and density of plant species often vary considerably between adjacent areas due to differences in factors that influence plant productivity (e.g., soil type, topographic position, and slope angle; Clark

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et al. 1998), even when rainfall and temperatures are similar. Hence, in order to develop adequate conservation plans and management strategies for endangered primate species, it is crucial to study habitat use patterns in relation to the distribution of essential food resources (e.g., Wasserman and Chapman 2003; Terada et al. 2015).

Optimal foraging theory predicts that individuals should preferentially use areas where foraging efficiency is highest (MacArthur and Pianka 1966), and it postulates that primates may adjust their foraging behavior to meet their nutritional needs in response to changes in the availability and distribution of food and other resources (Charnov 1976). When faced with a choice of habitat types, primates usually prefer areas where food resources are more abundant (e.g., O'Brien and Kinnaird 1997), since an abundance and high diversity of food species may assure the maintenance of a selective diet (e.g., Stoner 1996). Studies on endangered primates inhabiting karst habitats generally describe karst forests as nonpreferred habitats, likely due to the inadequate food resource availability in these forests (for white-headed langur, *Trachypithecus leucocephalus*, see Li and Rogers 2005; for Delacour's langur, *Trachypithecus delacouri*, see Workman 2010). In their study of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of East Kalimantan (Indonesia), for example, Marshall et al. (2007) suggested that the relatively low tree species diversity of limestone karst forest may explain why orangutans avoid these areas, and they concluded that karst forest should be considered suboptimal habitat.

Anthropogenic habitat disturbance can also affect primate spatial and habitat use (e.g., Hoffman and O'Riain 2011; Riley 2008; Santhosh et al. 2015) by creating trade-offs between perceived risk and fitness-enhancing activities (see Frid and Dill 2002 for a review). For example, the pygmy marmoset (*Cebuella pygmaea*) shifted to the upper canopy in areas disturbed by ecotourism but used the lower strata in less-disturbed areas (de la Torre et al. 2000). Similarly, Sulawesi crested black macaques (*Macaca nigra*) responded to approaching groups of tourists by splitting up and retreating into the trees or fleeing (Kinnaird and O'Brien 1996). Accordingly, the occurrence of primate populations in karst forests has often been explained in terms of using limestone formations as a refuge from surrounding human disturbance, rather than as an ecological dependency. For example, white-headed langurs live in inaccessible and safer karst habitat, even though this habitat provides fewer preferred foods (Li and Rogers 2005), while François' langurs (*Trachypithecus francoisi*) and Cat Ba langurs (*Trachypithecus poliocephalus poliocephalus*) spend more time in the plains or other areas that are accessible to humans only when food becomes scarce (Zhou et al. 2013; Hendershott et al. 2018).

The moor macaque (*Macaca maura*)—which is currently listed as Endangered (A2cd) by the IUCN, mainly due to

habitat disturbance and fragmentation (Evans et al. 2001; Riley 2010; Supriatna et al. 2008)—is also a karst-dwelling primate in the southwest peninsula of Sulawesi, Indonesia. In this area, well-preserved forests present a highly fragmented distribution (Kessler et al. 2005), since most of the lowland tropical rainforest has been modified by increasing human encroachment and activities (i.e., pastures, cropland, agroforestry) (Cicuzza et al. 2011). Although moor macaques have been observed in a variety of habitats ranging from humid and deciduous forests to grassland (Supriatna et al. 2008) and sandy beaches (AA and N. Babo, pers. obs.), residual populations are now extremely fragmented and increasingly restricted to the karst forests. Here, the dissolution of Tertiary limestone layers has created a heterogeneous karst landscape that includes fragments of some of the most intact forests of the entire southwestern Sulawesi (Canon et al. 2005). This area has been proposed as a UNESCO World Heritage site due to its importance for biodiversity conservation (King 2015).

Several studies of moor macaque social behavior have been carried out, in addition to a few studies on their reproductive biology and feeding ecology (Watanabe and Brotoisworo 1982; Matsumura 1991, 1993, 1998; Okamoto and Matsumura 1998; Okamoto et al. 2000; Okamoto and Matsumura 2001, 2002; Sagnotti 2013; Riley et al. 2014; Morrow et al. 2019). However, moor macaque use of karst habitat has never been thoroughly investigated, likely due to the harsh nature of karsts and hence the difficulty involved in accessing all of the areas within a karst forest. Our objective in this study was to fill this gap in knowledge by assessing the suitability of potentially different (in terms of forest structure and composition) karst forest habitats and by observing, for the first time, the activity and habitat use of moor macaques in the entire karst forest environment.

Studies conducted in other karst environments have found that plant species do not grow evenly due to differences in water and soil availability between adjacent areas (Xu 1993). Accordingly, at our study site, we predicted that the forest on soil-rich plains or barely inclined slopes would provide a greater abundance and diversity of macaque food species (Jiang 1997) than the forest on the soil-poor karst towers. Secondly, as also observed for other primate species inhabiting limestone forests (see Huang et al. 2008 for the white-headed langur and the François' langur; see Schneider et al. 2010 for the Cat Ba Langur), we predicted that moor macaques would differentially use the plain forest and karst tower forest. Specifically, because of the expected differences in macaque food availability across the overall karst habitat, we predicted that feeding activities would occur more frequently in the karst plain forest compared to the karst tower forest. We also predicted that moor macaques would spend more time in the plain forest, where food resources are expected to be more abundant.

## Methods

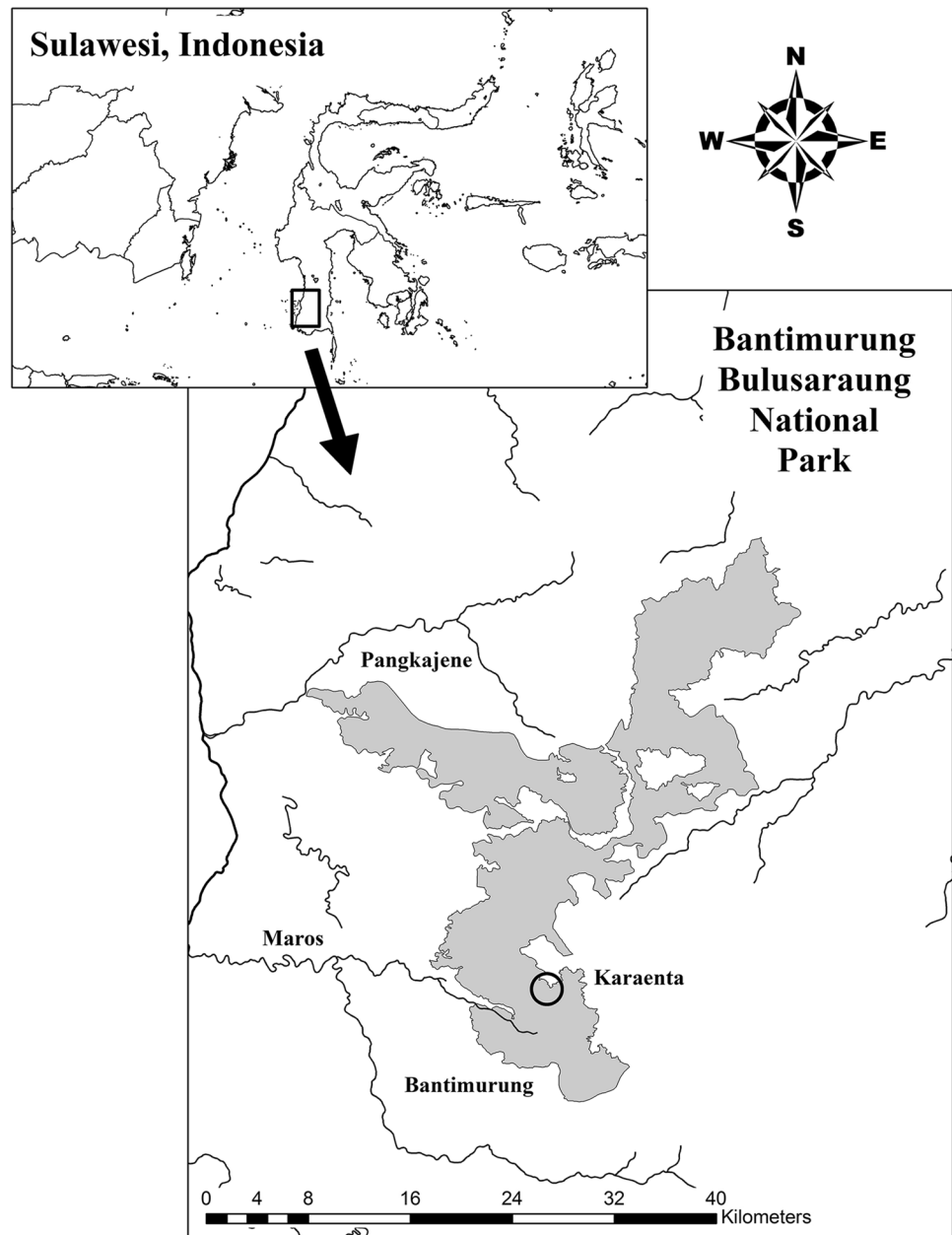
### Study area and subjects

The study took place in the Karaenta area, a former nature reserve that is approximately 1000 ha in size and situated in Bantimurung Bulusaraung National Park (BABUL-NP), in South Sulawesi Province, Indonesia (Fig. 1). Our study site was situated at 258–362 m a.s.l. and was approximately 60 ha wide. Locally, the karst forest reflects the overall complexity of karst morphology; there are a range of potential habitats. Karst towers that rise up to 70 m

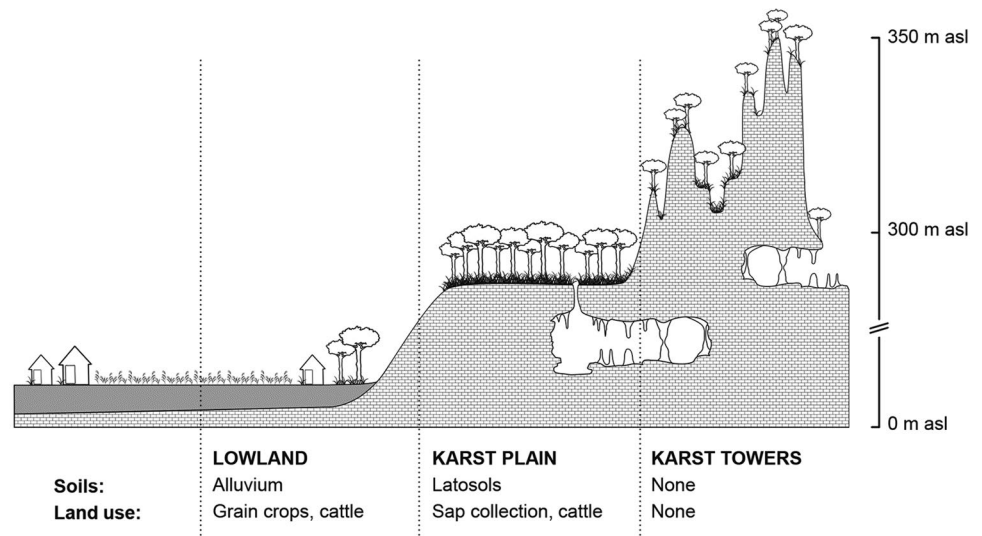
from the ground are intermingled with the forest (Fig. 2). The vegetation exemplifies some of the best-preserved forest patches of the entire South Sulawesi province and appears to be representative of typical karst forests, with a rather open vegetation structure and an abundance of pioneer and weedy species (Cannon et al. 2005).

We conducted observations on two habituated social groups, namely groups B and G. At the time of this study, group B comprised  $30 \pm 1$  individuals ( $N_{\text{adult males}} = 4$ ,  $N_{\text{adult females}} = 8$ ,  $N_{\text{juveniles/subadults}} = 18 \pm 1$ ,  $N_{\text{infants}} = 1-2$ , as the number of infants differed across the study period). From 1981 to 1992, group B was frequently provisioned for research purposes (see Okamoto et al. 2000). From 1992 to

**Fig. 1** Bantimurung Bulusaraung National Park (*shaded area*) and the Karaenta study area (*black circle*) in Sulawesi, Indonesia



**Fig. 2** A cross-section of the geology of the study area. Alluvium (quaternary marine sedimentary rocks) is shown in *dark gray*; limestone (tertiary carbonates) is depicted in *light gray*



2010, group B was occasionally provisioned for tourism and media purposes (one or two times per month) by park staff, and from 2010 to 2012 it was again provisioned three or four times per week for research purposes. However, after 2012, park staff were discouraged from provisioning the group to avoid affecting data collection, and group B was not provisioned by researchers or park staff during the observations performed for this study. Group G comprised  $18 \pm 1$  individuals, ( $N_{\text{adult males}} = 2$ ,  $N_{\text{adult females}} = 4$ ,  $N_{\text{juveniles/subadults}} = 12 \pm 1$ ,  $N_{\text{infants}} = 2-3$ ). The habituation of group G took place in 2014 and 2015 (Hanson and Riley 2018) and continued from March to May 2016. We began formal observations on group G after a suitable level of habituation that allowed a monkey-to-observer mean observation distance within the range of that for group B individuals. We focused our observations on individually recognized adults, for a total of 18 study subjects.

## Data collection

### Habitat structure, composition, and level of anthropogenic disturbance

In order to estimate the karst area within the study site, we mapped the karst tower formations by means of GPS (Garmin GPSMap64s) and GIS (Esri, ArcGIS) technologies. To assess vegetation structure and composition, we established 50 plots ( $20 \times 10 \text{ m}^2$ ; a total of  $10,000 \text{ m}^2$  sampled) using a randomly stratified approach in order to obtain 25 plots in the low forest (on karst plains) and an equivalent number of plots on top of the karst tower formations (Fig. 2). In each plot, we identified and measured each tree and liana with  $\text{DBH} \geq 5 \text{ cm}$  (Hédél et al. 2009). We chose a threshold of 5 cm instead of the standard 10 cm because we noted that there were reproductive parts on young plants as

well. Within each plot, we recorded the percentage cover of trees with  $\text{DBH} \leq 5 \text{ cm}$ , shrubs, and herbaceous plants in two subplots ( $5 \times 5 \text{ m}$  each, for a total of  $1250 \text{ m}^2$ ). Plant species identification was the outcome of a collaborative effort between one of the authors (PON) and the Herbarium Bogoriense (Indonesian Institute of Science, Bogor, Indonesia), with the support of a local flora guide (Whitmore et al. 1989) and data from a previous field study (Sagnotti 2013). We measured the altitude of each plot by means of GPS, and we visually estimated slope angle as well as area percentages of soil, outcrops, stones, and plant litter. We also estimated the percentage of overstory canopy closure in each plot by means of a convex spherical densitometer. We collected qualitative data (presence/absence) on anthropogenic habitat disturbance within each plot, noting any trace of human activity (i.e., human trails, garbage, and small-scale forest use, which in this study included wood cutting and sap collection from *Arenga* palms). We collected plot data from September 2014 to February 2015, and then again from April to September 2016.

### Behavioral observations

AA and LG collected behavioral data on group B from September 2014 to February 2015, while AA and an assistant collected data on group G from June to November 2016. Due to the need to pool data, and in order to prevent observer bias, data collection was initiated after reaching interobserver reliability kappa scores of more than 0.81 (defined by Viera and Garrett 2005 as “almost perfect agreement”) when identifying (a) study subjects, (b) behaviors, and (c) positions in the karst forest. We collected behavioral data by following the monkeys 5 days per week for 6–12 h per day. Six-hour sampling days were planned, with morning collection and afternoon collection



performed on alternate days to obtain a set of observations that were uniformly distributed throughout the day, from dawn to dusk. Every 30 min, we conducted a 10-min group scan (Martin and Bateson 1993), during which we recorded the first behavioral activity that lasted for at least 5 s for each individual located (e.g., Kinnaird 1990; Riley 2007). We collected 580 scan samples for group B and 591 scan samples for group G, totaling 195 observation hours. Behavioral activities were defined as feeding (consumption of food, including mastication), foraging (searching for and processing food), locomoting (moving more than 2 m in 5 s), social interactions (any of allogrooming, sexual, playing, and agonistic behaviors; see Thierry et al. 2000), and resting (none of the previously mentioned behavioral activities). When an individual was feeding on plants, we determined the species and the part of the plant consumed, and if it was involved in both food-related activities and another activity, we scored the feeding behavior. In addition, we recorded the position in the karst forest of each individual sampled in terms of height from ground (0 m, 0–2 m, 2–10 m, 10–20 m, > 20 m) and substrate (soil, rock, tree). Visibility was comparable in the two groups' home ranges. GPS coordinates of group position were recorded every 30 s for 20 min between scans to increase the accuracy of the home range estimation (e.g., Campos et al. 2014).

## Data analysis

We constructed a matrix comprising 173 rows (trees, shrubs, and herbaceous species) and 50 columns (plots) to test for similarities among the 50 plots using multivariate analysis procedures (cluster analysis). Numerical classification was implemented using a group-average algorithm based on relative Euclidean distances (Orlóci 1979) (PcOrd 5.0 package, McCune and Mefford 2006). To test the ecological consistency of the cluster analysis results (to possibly detect different types of habitats), we compared the derived groups in terms of altitude, slope angle, outcrop, stones, soil, plant litter, dead wood, and canopy closure. For this purpose, the data matrix (see Table S1 in the Electronic supplementary material, ESM) was subjected to a detrended correspondence analysis (DCA) (McCune et al. 2002). In addition, we tested for differences between the DCA clusters in terms of forest structure by analyzing a variety of plot data such as plant species diversity and tree density, DBH, and canopy closure for all species. We analyzed tree species diversity (a combination of richness and relative abundance) via the Shannon–Wiener index ( $H'$ ) and tested for differences between habitats ( $H'_1 - H'_2$ ) via the Hutcheson  $t$  test (e.g., Magurran 2004), where the  $t$  test statistic is given by

$$t = \frac{H'_1 - H'_2}{\sqrt{\text{Var } H'_1 + \text{Var } H'_2}}$$

We tested the two habitats for median differences in tree density and DBH via the Wilcoxon signed-rank test (using species as the unit of analysis), and for mean difference in percent canopy closure via two-tailed  $t$  tests (using plot as the unit of analysis). We replicated the same analyses to test for further differences between the DCA clusters in terms of moor macaque food species attributes, as defined by species diversity, tree density, and DBH, including key food tree density. We defined key food species as those that cumulatively accounted for 95% of the total feeding time. We also compared levels of anthropogenic disturbance (in terms of presence/absence of human traces) between the clusters.

We estimated the total home range areas (95% isopleth) and core areas (50% isopleth) from GPS coordinates by means of movement-based kernel density estimation to increase biological realism (e.g., Campos et al. 2014), with bandwidth computed specifically for the input dataset using a spatial variant of Gaussian approximation. We calculated the per capita area by dividing the overall home range size by the mean number of adult individuals in each group. To assess within-group differences, we collated the scan sampling data on behavioral activities with those on individuals' positions in the karst forest. We used repeated measures ANOVA with a permutation test (and mean per individual as the unit of analysis) to determine whether the activity budget of each group varied in relation to habitat cluster (Frossard and Renaud 2018). To assess between-group differences, we used an ANOVA with a permutation test for unbalanced designs (Legendre 2007) to determine whether the two groups differed in the proportion of time spent in each habitat cluster as well as in the proportion of time devoted to daily activities. We used a  $\chi^2$  test to determine whether habitat use (i.e., proportion of time spent) by the two groups differed significantly from expected values derived from the actual proportion of habitat clusters within the home ranges.

All dependent variables were tested for normality via the Shapiro–Wilk test and for homoscedasticity via the Levene test before analyses. Nonparametric tests were chosen over parametric ones when the data deviated from a normal distribution. We considered results to be statistically significant when  $p < 0.05$ . All statistical tests were performed using RStudio software, version 3.5.3 (R Development Core Team 2019). All GPS data (both topographic and home range data) were elaborated in ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, CA, USA), with data projected onto the Universal Transverse Mercator (UTM) coordinate system (datum WGS 1984; zone 50S) and cell size output set to 3 m.

## Results

### Karst habitats: karst plain forest and karst tower forest

In the sampled area (1 ha), we identified 173 plant species (trees, shrubs, and herbaceous) belonging to 72 families. We identified 98 species as macaque food species, 17 of which were key food species (Table S2 in the ESM), and five consumed plant parts (fruits, leaves, stems, sprouts, and flowers). Tree identification was accurate to the species level in 115 cases, and to the genus level in 14 cases. The identification of herbs and shrubs was accurate to the species level in 37 cases and to the genus level in seven cases.

The dendrogram obtained from the classification procedure highlighted the existence of two main clusters characterized by different species assemblages (Fig. S1 in the ESM). The specific compositions of the two clusters closely corresponded to the 25 plots in the forest on the karst plain (karst plain forest; “KPF” hereafter) and the 25 plots in the forest on the tops of the karst tower formations (karst tower forest; “KTF” hereafter), respectively. We identified 127 species (64 families) in the KPF and 119 species (53 families) in the KTF. Less than half of the species found (42%) occurred in both the KPF and the KTF; the other 58% were only found in either (not both) of the clusters [see Table S3 in the ESM for high-frequency species that were common to the KPF and the KTF or were only found in either habitat; see Keßler et al. 2002 and The International Plant Names Index (The Plant Names Project 2017) for nomenclature details]. The detrended correspondence analysis (DCA) supported the detection of two distinct habitats by identifying the abundance of soil and the density of canopy closure as discriminant factors for the KPF and high values of slope, outcrop, and altitude as discriminant factors for the KTF (see Fig. S2 in the ESM).

### Forest attributes, tree characteristics, and level of anthropogenic disturbance

In the sampled area, we identified 107 tree species belonging to 48 families. We identified 74 tree species as macaque food species and 14 as key food species. We identified 81 tree species (42 families) in the KPF and 64 tree species (32 families) in the KTF. We identified 61 tree species as food species in the KPF, 12 of which were key food species, and 42 tree species as food species in the KTF, four of which were key food species. Tree species diversity was greater in the KPF than in the KTF for all species ( $H'_{\text{KPF}} = 3.913$ ,  $H'_{\text{KTF}} = 3.345$ ; Hutcheson  $t$  test,  $t =$

$-9.528$ ,  $df = 909$ ,  $p < 0.001$ ) and for macaque food species ( $H'_{\text{KPF}} = 3.682$ ,  $H'_{\text{KTF}} = 2.994$ ; Hutcheson  $t$  test,  $t = 11.186$ ,  $df = 789$ ,  $p < 0.001$ ). Total tree density and food tree density did not differ significantly between the KPF and the KTF (Wilcoxon signed rank test,  $W = 2963.5$ ;  $p > 0.05$ ;  $W = 1317.5$ ,  $p > 0.05$ , respectively); however, key food tree species density was significantly greater in the KPF than in the KTF (Wilcoxon signed rank test,  $W = 2.1618$ ;  $p < 0.05$ ). Percent overstory density was greater in the KPF than in the KTF (KPF =  $84.76\% \pm 1.69$ , KTF =  $63.25\% \pm 3.76$ ; 2-tailed  $t$  test,  $t = -4.61$ ,  $df = 48$ ,  $p < 0.001$ ). Average tree DBH was larger in the KPF (mean = 14.4 cm,  $N = 416$ ) than in the KTF (mean = 10.9 cm,  $N = 915$ ) (Wilcoxon signed rank test,  $W = 3929.5$ ,  $p < 0.001$ ), as was average DBH if limited to food tree species (KPF mean = 14.19 cm,  $N = 348$ ; KTF mean = 11.38 cm,  $N = 728$ ; Wilcoxon signed rank test,  $W = 2004.5$ ,  $p < 0.001$ ). Traces of anthropogenic disturbance were only found in the KPF. Forest structure, food tree species attributes, and degree of anthropogenic disturbance are summarized for KPF and the KTF in Table 1.

### Macaque activity budget, home range, and habitat use

Home ranges, core areas, and proportions of the habitats within the home range differed between the two study groups. Group B's home range (21.53 ha) and core area (6.11 ha) were greater than group G's (17.9 and 4.39 ha, respectively). Group G, however, had a greater per capita area (0.99 ha) compared to group B (0.72 ha). While both habitats were included in each group's home range, the proportions of those habitats differed according to the group considered: KPF<sub>B</sub> 66%, KTF<sub>B</sub> 34% compared to KPF<sub>G</sub> 35%, KTF<sub>G</sub> 65% (see Fig. 3). As predicted, both groups spent more time feeding when in the KPF (ANOVA, group B:  $F = 6.13$ ,  $p = 0.037$ ; group G:  $F = 28.22$ ,  $p = 0.0036$ ) than when in the KTF. The percentage of time devoted to remaining activities (foraging, locomotion, social interactions, and resting) did not differ between habitats. Group B spent more time in the KPF than group G did (ANOVA,  $F = 590.3881$ ,  $p < 0.001$ ), whereas group G spent more time in KTF than group B did (ANOVA,  $F = 481.833$ ,  $p < 0.001$ ). Based on the proportions of KPF and KTF within each home range, a chi-square test revealed that group B ( $\chi^2 = 34.899$ ,  $df = 1$ ,  $p < 0.001$ ), but not group G ( $\chi^2 = 3.253$ ,  $df = 1$ ,  $p = 0.071$ ), used the KPF more than expected (Fig. 4). Group B foraged more than group G (ANOVA,  $F = 8.306$ ,  $p = 0.009$ ), while group G fed more than group B (ANOVA,  $F = 11.827$ ,  $p = 0.008$ ). No between-group differences were detected for the other daily activities (locomotion, social interactions, and resting) (Fig. S3 in the ESM).

**Table 1** Forest structure, macaque food species attributes, and proportion of plots with traces of anthropogenic disturbance for each habitat

Habitat features	Karst plain forest (KPF)	Karst tower forest (KTF)
Forest structure		
Tree species diversity ( $H'$ )**	3.91	3.35
Tree density (trees/ha)	832 ± 66.45	1830 ± 169.90
Mean DBH of all trees (cm) **	14.40 ± 0.69	10.90 ± 0.58
Overstory density (%) **	84.76 ± 1.69	63.25 ± 3.76
Food species attributes		
Tree food species diversity ( $H'$ )**	3.68	2.99
Food tree density (trees/ha)	696 ± 60.75	1456 ± 160.78
Key food tree species density (trees/ha)*	188 ± 30.18	72 ± 18.95
Mean DBH of food trees (cm)**	14.19 ± 0.80	11.39 ± 0.66
Anthropogenic disturbance		
Presence of human trails	21/25 (0.84)	0/25 (0)
Garbage	10/25 (0.29)	0/25 (0)
Small-scale forest use	5/ 25 (0.2)	0/25 (0)

Standard error values shown after mean values

\*  $p < 0.05$

\*\*  $p < 0.001$

## Discussion

The present study provides the first detailed description of the limestone ecosystem of South Sulawesi that likely hosts the majority of the remaining populations of the endangered moor macaque. Our results indicate the occurrence of two clearly distinct habitats within this heterogeneous ecosystem, namely the karst plain forest (KPF) and the karst tower forest (KTF), both of which are used by the macaques in their daily activities. These two habitats differ in site topography (soil, slope, outcrop, altitude), vegetation structure (tree DBH, canopy closure), and composition (species frequencies and proportion of exclusive taxa), as well as in the abundances and distributions of food species. As previously reported for other karst areas (Xu 1993; Jiang 1997), we found that the plain forest in our study area is characterized by a higher species diversity, a larger tree size, and a denser canopy closure than the tower forest. In terms of macaque foods, the plains are characterized by a higher number, greater diversity, and larger mean DBH of food species, as well as a higher density of key food species.

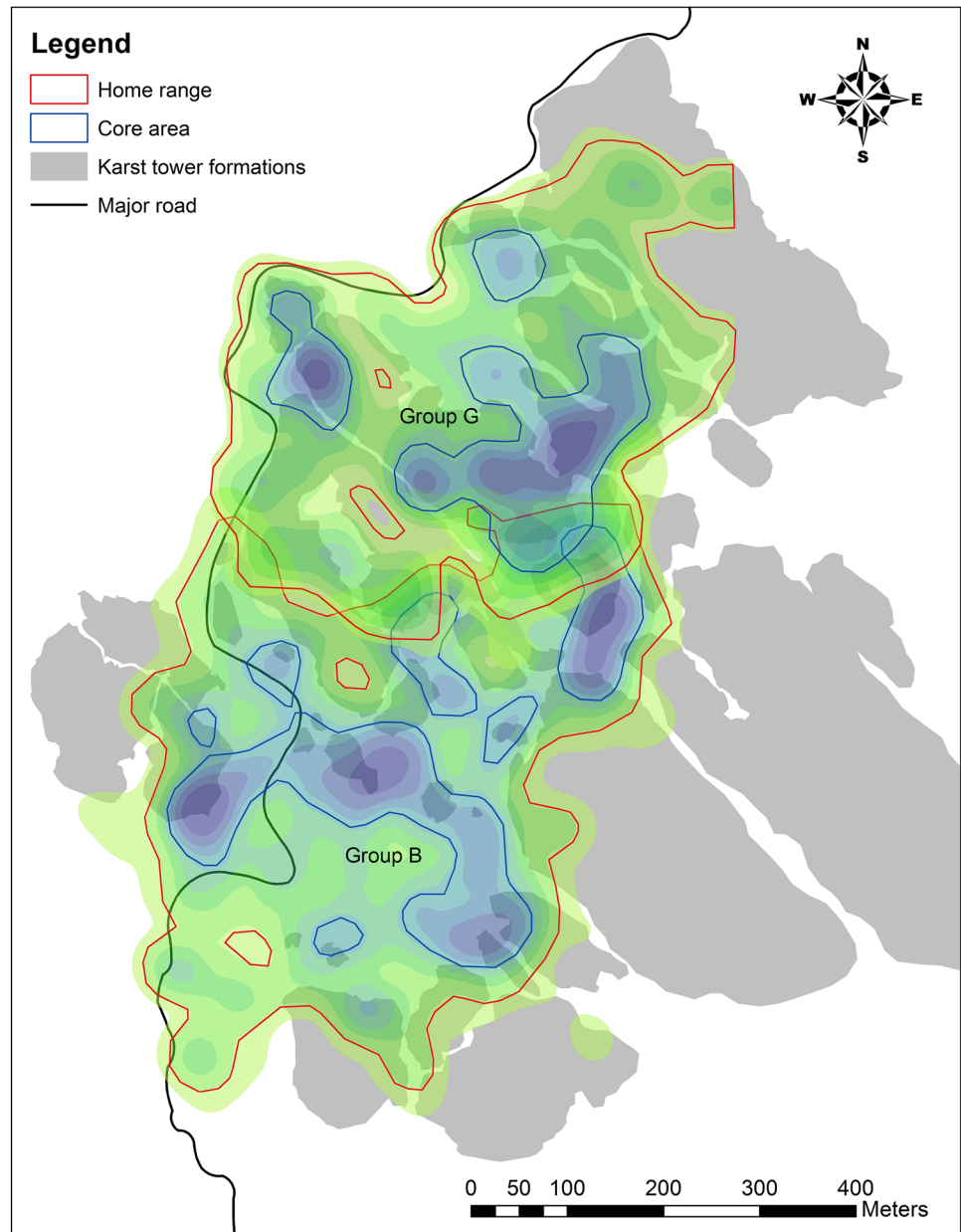
Following other studies documenting a correlation between dietary richness and differences in vegetation richness between habitats (Li et al. 2003), our results suggest that the KPF likely provides the macaques with more feeding opportunities than the KTF does, and our finding that the macaques spent more time feeding in the more productive KPF further supports this conclusion. Overall, our results are consistent with those previously reported for other limestone primates. For example, the white-headed langur in the karst areas of southern Guangxi (China) spent 65.05% of its feeding time in the bottom zone, which also had the highest

food density (Huang 2002), and the Cat Ba Langur in northern Vietnam increased its foraging activity considerably in the lower elevations, likely due to the abundance of food resources in the lower parts of the hills (Schneider et al. 2010). Thus, our results suggest that the KPF habitat may be a crucial portion of the landscape for ensuring the survival of moor macaques in South Sulawesi.

Our results also suggest that the probability of encountering human beings is higher in the KPF than in the KTF, and that the absence of human traces in the KTF may make it a valuable refuge for the macaques, as it is a less risky portion of their home range. Given that large predators typical of islands west of Wallacea are absent in Sulawesi (O'Brien and Kinnaird 2000), predation pressure in Sulawesi is reported to be low (e.g., van Schaik 1989); however, humans represent a real threat to Sulawesi macaques in that these macaques are reportedly hunted, poisoned, trapped, and kept as pets (e.g., Lee 1999; Busaeri et al. 2015). Although the two groups ranged in areas that included both KPF and KTF, our results show that group B's home range included more KPF than KTF habitat, while the opposite was found for group G's home range. In addition to that, group B spent more time in the KPF than group G did, and spent more time there than expected from the proportion of KPF included in its home range. Group B's use of the more productive but riskier habitat may be due to its past history of provisioning, which may have allowed its individuals to be less fearful of encountering human beings in comparison with group G, whose individuals have never experienced provisioning.

Another possible explanation for the observed intraspecific variation in habitat use could be the difference in the sizes of the two groups: in socially foraging animals, as

**Fig. 3** Home ranges and core areas of group G (*top*) and group B (*bottom*) in relation to tower karst formations. The *white areas* represent the karst plain forest



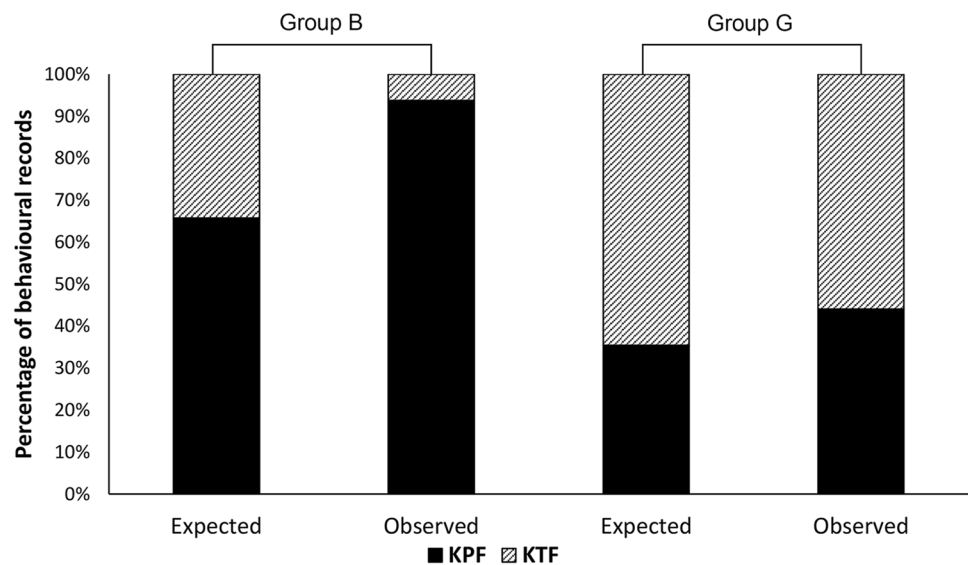
group size increases, an individual can devote less time to vigilance and thus more time to foraging in areas perceived as risky (e.g., Lima 1995; Ale and Brown 2007). For example, in baboons (*Papio cynocephalus ursinus*), as group size increased, foraging occurred farther from natural refuges (Cowlshaw 1997), and in long-tailed macaques, large groups spent more time than small groups in low forest strata, where the risk of terrestrial predators was greater (van Schaik et al. 1983). Because the home ranges of groups B and G overlapped and agonistic interactions between these groups have been observed (AA, pers. obs.), it is also possible that the larger group B had a competitive advantage over group G, thereby enabling it to spend more time in the more productive KPF. However, further research with

additional groups is needed to assess the effect of group size, as well as how the potentially differing levels of between-group and within-group competition experienced by the two groups may affect habitat use and the activity budget (c.f. van Schaik et al. 1983; Ganzhorn 1988).

In conclusion, our results indicate the occurrence of two habitats characterized by distinct ecological features in the karst forest of South Sulawesi, both of which are used by moor macaques. The accessible and productive plains (KPF) provide the majority of the food options for the macaques, but also an opportunity for human small-scale forest use for subsistence needs (Busaeri et al. 2015). On the other hand, the inaccessible and less productive karst towers (KTF) likely provide a natural refuge from the surrounding human



**Fig. 4** Expected vs. observed percentages of behavioural records associated with the KPF and the KTF, based on the proportion of each habitat within each group's home range



disturbance. In this context, moor macaques appear to be ecologically flexible—able to exploit the karst forest as a whole and able to cope with human disturbance, in accordance with what is known for other members of the genus *Macaca* (e.g., see Riley 2007 for *M. tonkeana*; see Yanuar et al. 2009; Ruppert et al. 2018 for pig-tailed macaque *Macaca nemestrina* and long-tailed macaque). Nevertheless, habitat disturbance and fragmentation still represent major threats to moor macaques, so karst forest protection should be considered as part of the ongoing conservation strategy aimed at ensuring the long-term persistence of the species. In addition, repeated interactions with humans, even if non-threatening, could also result in human-mediated behavioral spillover, which could in turn become maladaptive (Ménard et al. 2014; Geffroy et al. 2015). For this reason, future efforts should focus on balancing the needs of both humans and nonhuman primates for the KPF by monitoring human activities, managing the emerging human–macaque interface (see Morrow et al. 2019), and developing conservation education programs for local people and visitors.

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