Population density and abundance of long-tailed macaques (*Macaca fascicularis*) in Puerto Princesa Subterranean River National Park, Palawan, Philippines

This study is one of the first attempts to establish baseline data and address knowledge gaps pertaining to the population, distribution, and parasite ecology of long-tailed macaques in the Philippines, specifically in the Palawan region. Ten line transects with a ground length of two kilometers each were established in the Puerto Princesa Subterranean River National Park (PPSRNP). Transect work included habitat assessment, census walks, and collection of fecal samples of long-tailed macaques in PPSRNP. Assessment of habitat was done via point transect sampling where detailed habitat measurements were taken for every 250-meter sections of each transect. For census walks each transect was visited twice, starting surveys at exactly 0600. Perpendicular distances and geographic coordinates of each sighting, as well as the number of groups and the corresponding group sizes of encountered macaques were noted within a sampling time of 10 to 15 minutes. Group and individual count data were then analyzed using DISTANCE and the Kelker method to determine density and population size of long-tailed macaques within PPSRNP. Analysis of count data meanwhile yielded a population density of 0.2 individual per square kilometer (or 1 individual per 5 sqkm) and an estimated population size between 967 – 2,633 individuals based on average values from the analysis of group count data via Kelker method and DISTANCE.

KEYWORDS: long-tailed macaques; population; anthropogenic disturbance; Palawan.

INTRODUCTION

The need for baseline data on population ecology for many species of wild animals has been increasing as forests have been under pressure for the extraction of valuable derivatives such as timber, mineral, and animal resources. Activities brought by land use change have resulted to habitat fragmentation, particularly degradation of native habitats, and the fauna and flora associated with these regions (Altman *et al.,* 1981).

In the case of primates, population studies are valuable for conservation in that it provides: 1) baseline density or total number that can be monitored in the future; 2) an assessment of the importance of different habitats for primate conservation; 3) an assessment of changes in numbers since a previous census period and; 4) an assessment of population trends if censuses are carried out frequently enough (Plumptre and Cox, 2006). Establishing baseline information on the distribution, abundance, and trends of primate populations is a vital step in primate conservation since population monitoring enables direct measurement of the effect of local threats and assessment of the effectiveness of conservation measures. The identification of priority areas for protection, development of conservation management strategies, mitigation of threats, and balancing of economic and conservation priorities are also in the mercy of availability of adequate data such as a quantitative baseline of primate populations (Campbell *et al.,* 2016).

The long-tailed macaque (*Macaca fascicularis*) is the only species of non-human primate in the Philippines and is known to have the widest geographical range of any primate species. It has several subspecies variation across Southeast Asia and is infamous for its abundance and ecological resiliency (Gumert, 2011). In the Philippines, long-tailed macaques are found in almost all major land masses (Luzon, Visayas, and Mindanao) where two subspecies, *M.f. fascicularis* and *M.f. philippinensis*, range from being locally common to uncommon (Ong & Richardson, 2008). Long-tailed macaques in the country were in high abundance prior to 1960s until trapping and forest conversion practices drove the decrease in wild populations (Fooden, 2006). However, despite being widespread, there is a lack of studies on current population estimates and distribution of long-tailed macaques in the country.

The main objective of this study is to estimate the population density and abundance of long-tailed macaques in Puerto Princesa Subterranean River National Park by analyzing line transect data through traditional (Kelker method) and modeling (DISTANCE) methods. Specifically, this study aims to 1) obtain estimates of group density, group size, and total population size of the species, and 2) associate population estimates with anthropogenic disturbances observed in PPSRNP.

METHODS

Preliminary Activities

Acquisition of mandatory permits and presentation of proposal to the local government of Puerto Princesa City and the Protected Area Management Board of PPSRNP were accomplished prior to fieldwork. Fieldwork for this study was conducted under Wildlife Gratuitous Permit No. 2016-04, which was released on March 9, 2016. All necessary permits were approved by the Palawan Council for Sustainable Development Staff (PCSDS).

Study Site and Establishment of Transects

The Puerto Princesa Subterranean River National Park (PPSRNP) is a recognized World Heritage Site (Criteria viii and x) having lowland forests with maximum altitude of approximately 800 meters above sea level. Ten line transects were primarily identified on a digital map of PPSRNP to serve as guide in the planning and establishment of transects. Each transect line has a ground length of 2 kilometers, with no particular width due to differing broad habitat types (Mallari *et al.*, 2009). The transects were positioned with a distance not less than 100 meters. In areas with dense understory vegetation, trails with a width not exceeding a meter were created. Common foot trails were avoided as much as possible in order to satisfy the assumptions of the distance sampling survey design. Pilot surveys (approx. 2 days) of each transect were done prior to the survey proper to allow necessary cutting of vegetation, standardize distance estimation, and acclimatize with the trails.

Population Survey

Field surveys were conducted over a month-long duration during the dry season. The survey design followed the basic assumptions of line transect sampling with particular reference to surveys of primates that occur in groups (Buckland *et al.*, 2010; Marshall *et al.*, 2008). All individuals encountered along the transect were recorded within a 10- to 15-minute sampling time to prevent overestimation of density owing to additional groups entering a focal group and double counting (Marshall *et al.*, 2008). The following variables were recorded during line transect sampling: (a) meteorological or environmental parameters (e.g. time of day, weather conditions), (b) perpendicular distance from the line to each detected individual, (c) perpendicular distance from the line to the center of a group, if macaques happen to occur in groups during detection, (d) number of groups and their respective group size in case of detection of multiple groups, and lastly, (e) height in vegetation of detected individuals/troops.

Each transect was visited twice (from 0 meter to 2000 meters and vice versa) throughout the study period, with a one-way sampling effort of two kilometers, traversed at a minimum speed of one kilometer per hour starting at strictly 0600. Whenever an individual or a group of macaques is detected, the perpendicular distance from the center of the group and from each distinct individual were estimated and recorded. Also, in instances where visually-detected macaques flush in response to the observers, the distance from the point where they flush were estimated. Talking among observers and other unnecessary noise were also not encouraged during census walks to avoid compromising detection. The approximate locations of detected individuals/groups of macaques were also marked using a Garmin Ltd. eTrex 30x GPS receiver. Perpendicular distances from group centers and from each individual were pooled separately to be used in extrapolating mean group size, population density, and population size using traditional (Kelker method) and modeling approaches (DISTANCE program).

Data Analysis

Kelker Method

For the Kelker-based perpendicular distance method (National Research Council, 1981), mean group size and population density were estimated using the following equation:

$$D = n/2La$$

wherein D = density of individuals or groups per unit area, n = number of individuals or groups detected along a transect, L = total length of the transect, and a = half the effective strip width.

The factor a is a location and species-specific cutoff point that determines the area around the transect where the detection probability is assumed to be 1 (National Research Council, 1981). The effective strip width was determined by analyzing the distribution of perpendicular distances in a histogram – the histogram with a block width showing the clearest cutoff point (a) was selected and all sightings within the selected cutoff point were included in the calculations. For example, a cutoff point at 43 resulted to an effective strip width of 2 x 43 m. Mean group size was determined based on all groups detected within the effective strip width.

DISTANCE

In DISTANCE (v.7.1), the number of detected groups in each transect were pooled to calculate the encounter rate (individuals detected/transect ± standard error), group size. and macaque density (individuals/km^2 ± standard error) (Thomas *et al.*, 2010; Buckland *et al.*, 2001). Distance sampling uses individual counts and perpendicular distances as the main units for analysis (cluster size in some primate studies). Sampling effort of line-transect data on DISTANCE is defined as "the length of a line for each time it is sampled," (Buckland *et al.*, 2001) hence the two-kilometer minimum sampling effort per transect. All data were truncated at the largest 5% of the distances to remove outliers (Buckland *et al.*, 2010).

For both conventional (CDS) and multiple covariates distance sampling (MCDS) analyses, two key functions namely the half-normal and hazard-rate models were used with three adjustment types (e.g. cosine, simple polynomial, and hermite polynomial series). Density estimates and other population parameters were retrieved from the model which yielded the minimum Akaike Information Criterion (AIC) value (Thomas *et al.*, 2010; Buckland *et al.*, 2001).

RESULTS AND DISCUSSION

Line Transect Sampling of Long-tailed Macaques in PPSRNP

A total sampling effort of 40 kilometers yielded 38 group sightings comprised of 143 individuals are shown in Table 1. The most number of groups and individuals was recorded in T2, followed by T7, and subsequently by transects 1, 3, 5, and 9. Transects 4, 6, and 10 had the least number of detections, while no sightings were recorded in T8. These observations show that long-tailed macaques may occur as small groups or as individuals as they go about their activities between 0600 and 1000, since the number of groups do not necessarily indicate a congruent group size (number of individuals).

Table 1. Group and individual count data of long-tailed macaques detected during the dry-season census in PPSRNP

TRANSECT	NUMBER OF DETECTIONS	
	Groups	Individuals
T1	4	13
T2	8	49
T3	5	17
T4	3	6
T5	3	12
T6	4	7
T7	4	22
T8	0	0
T9	4	13
T10	3	4
TOTAL	38	143

During transect walks, most macaques were spotted in T2 (Jungle Trail-Camingay beach transect). The Jungle Trail, as the name suggests, is a 1.5-kilometer common foot path intended for tourists who choose to trek their way towards the mouth of the underground river. This trail is also used by bird watchers, forest rangers, tour guides, and other park staff to access several points of interest in the park (e.g. Central Park Station, Sabang Zipline, mangrove paddling area). The relative high number of detection in T2 was expected because the groups of macaques dwelling in this part of the park, as well as in T1 and T3, are habituated to humans that frequent the area. Meanwhile, detections in T5, T7, and T9 were also noteworthy despite of having remnants of and/or current land clearings (Table 2). For instance, the number of detections in T5 and T7 were comparable to transects where habituated macaques are observed (i.e. Transects 1-3) and could be accounted to the dominance of secondary forest habitats characterized in these transects, as discussed in the previous section. The detections in T9 could be mainly accounted to the location of the transect as it is closely-associated with tributaries of Babuyan River – an ideal environment for riparian and edge-dwelling species such as the long-tailed macaque (Muehlenbein, 2015). The least number of detections were recorded in T4, T6, and T10, all of which featured different signs of disturbance: a large-scale land clearing, zoning, and harvesting of almaciga resin, respectively. No detections were recorded in T8, a trail frequented by indigenous locals and is characterized with disturbance from shifting cultivation, but drifter macaques were observed outside transect boundaries.

Long-tailed macaques are also quite conspicuous within the vicinity of PPSRNP. They are initially sighted mid-story or in the forest canopy as the species is primarily arboreal. Macaques were mainly detected from their calls and movement through vegetation, while other indicators of presence include feeding signs on ground and feces and/or urine droplets on plants adjacent to possible roosting trees (Figure 1). Behavior also varied significantly within the surveyed transects. Habituation with humans was observed in individuals detected in T1 and T2 as these areas are closely-linked with foot trails used by tourists, park staff, and the locals. Elusive behavior (e.g. no warning calls or big movements) was particular in individuals detected in T5 and T7.

Fig. 1. A long-tailed macaque sighted in Panablan and some signs of macaque presence: feeding signs, signs of defecation/urination near roosting/ sleeping trees

Table 2 shows several habitat disturbances observed during transect walks at the PPSRNP. Harvesting of non-timber forest products appeared to be the most common as it was observed in all transects except T2. Slash-and-burn farming was observed in transects 5 to 10, particularly in T5, T6, T7, and T8 where large-scale clearings were documented. Poached animals such as squirrels, freshwater turtles, wild boar, and reticulated pythons were also noted in transects 7 to 10. Moreover, remnants of logging ca. 2007 (Puna, pers. comm.) were noted in transects 4, 5, and 6, while CADC markers and boundary fences were seen in T4 and T8 as these were known territories of indigenous groups dwelling within the PPSRNP. The regular influx of tourists in transects 1, 2, and 3 is noteworthy because fieldwork was conducted during the peak tourist season. An ongoing construction of a mini dam was also observed in T7, situated in Sitio Bayatao where a small community of lowlanders reside.

These disturbances may explain the number of sightings recorded in each transect; some anthropogenic activities can either keep macaques away or attract them towards a certain area subjected to a certain disturbance. For instance, the high number of individuals detected in T2, compared to neighboring transects 1 and 3 can be accounted to macaques being more accustomed to humans in T2 due to ecotoursim. The group of long-tailed macaques observed in T1 and T3 may be habituated but hostile to humans because the resident research team, forest rangers, and other park staff residing near these transects are quite annoyed of macaques due to garbage being ransacked or food being stolen from the rangers' station. Given the frequent contact of macaques with humans over the years, it is apparent that they have become habituated to humans in these transects, especially in T2. In fact, long-tailed macaques near T2 have learned to snatch plastic bags from visitors as they have associated plastic bags with food. This type of macaque-human interface has also been documented in several reserves and recreation parks in southeast Asia (e.g. West Java, Thailand, and Singapore) where long-tailed macaques are habituated and interact with tourists (Engelhardt, 1997; Aggimarangsee, 1992; Malaivijitnond *et al.,* 2005; Sha *et al.,* 2009a; Sha *et al.,* 2009b).

In contrast, the relatively high number of sightings noted from T7, despite being subjected to several anthropogenic activities, may be explained by the presence of water sources as suggested by the mini dam being built in the area. Similarly, T9 and T10 are essentially riparian areas and are thus ideal habitats for macaques, being closely-associated to tributaries of the Babuyan River. The low number of sightings in T10, however, can be accounted to its high location relative to T9 – perhaps because macaques prefer to spend longer hours in areas near T9 during daytime. Such observations correspond to early reports by Richard *et al.* (1989) who described the long-tailed macaque as a "weed" species that exploit early succession, riparian, and humanly disturbed areas, and much earlier by Kurland (1973) who noted that macaques tend to cluster around native villages on the rivers. Other studies denote *M. fascicularis* as a riverine "refuging" species (Hamilton and Walt, 1970) as they were observed to depart and return to a central place on a daily basis, usually near a river (Fittinghoff and Lindburgh, 1980; Wheatley, 1978, 1980, 1982; Sussman and Tattersall, 1986; van Schaik et al., 1996). According to Gumert *et al.* (2011), refuging is a unique behavior in long-tailed macaques in that it is rarely observed among primates, thus making the species a potentially interesting model for early human behavioral evolution.

Meanwhile, the CADC markers and boundary fences observed in T4 and T8 suggest that these areas are frequented by locals who may be preparing certain areas for cultivation or are harvesting non-timber forest products like rattan, vines, bamboo, and honey. Fresh signs of logging were also observed in some points along T4 that are close to boundary fences. In terms of slash-and-burn activities, the most notable clearings were observed in transects 5, 6, and 8, and which could explain the small number of sightings in these transects, particularly in T8 where no sightings were recorded. Large-scale land clearings and logging activities outside transects in Cabayugan and Marufinas were also

Table 2. Disturbances observed in selected areas in PPSRNP where transect walks and fecal sampling were conducted

TRANSECT	HABITAT DISTURBANCES						
	Logging (ca. 2007)	Slash-and-burn farming	Harvesting of NTFPs*	Poaching	Construction of mini dam / water reservoir	CADC** markers and wire fences	Ecotourism
T1	-	-	+	-	-	-	+
T2	-	-	-	-	-	-	+
T3	-	-	+	-	-	-	+
T4	+	-	+	-	-	+	-
T5	+	+	+	-	-	-	-
T6	+	+	+	-	-	-	-
T7	-	+	+	+	+	-	-
T8	-	+	+	+	-	+	-
T9	-	+	+	+	-	-	-
T10	-	+	+	+	-	-	-

*Non-timber forest products (e.g. rattan, almaciga resin, bamboo, vines, honey)
**Certificates of Ancestral Domain Claims

documented. These cleared areas for cultivation evidently lack potential sites for feeding and roosting; as a result, the macaques may resettle to other areas for subsistence. Wilson and Wilson (1975), for instance, noted the absence of long-tailed macaques in selectively-logged forests and were found to occur in primary lowland forest habitats. In the PPSRNP, it was observed that movement among macaque troops is mainly arboreal, while feeding occurs in small to large canopy trees for non-coastal and non-riverine habitats. This signifies the importance of a contiguous forest canopy since majority of their activities occur above the ground (Gumert et al., 2011).

Mean values of meteorological parameters are shown in Table 3. Mean sea level pressure is at 1011.23 hPa, mean temperature at 29.77 degrees Celsius, 72% relative humidity, average wind speed of 4 meters per second and some occurrences of haze, rain/drizzle, lightning and thunderstorms. Since field observations in PPSRNP occurred mainly during the month of April, the dominant weather condition is typical of the dry season in a Type I climate where two pronounced seasons occur: dry during the months of November to April and wet throughout the rest of the year. Western parts of mainland Luzon, Mindoro, Negros, and Palawan experience this climate as these areas are shielded by mountain ranges but are open to rains brought in by *habagat* and tropical cyclones (PIDS, 2005). Also, according to Galvin & Jones (2009), the climate in archetypal tropical rainforests in islands and peninsulas in Southeast Asia is characterized by seasonal rainfall and a relatively short dry season. Normally this dry season starts mid-March towards the first few weeks of May in the Philippines. The onset of the wet season occurred during the first week of May and was experienced during surveys in transects 9 and 10. Nevertheless, the weather condition during fieldwork is generally dry and is thus not too significant to explain the number of detections across transects.

Density and Group Size Estimates of Long-tailed Macaques Using DISTANCE and the Kelker Method

Table 4 shows the population parameters calculated both via DISTANCE and the Kelker method wherein the effective strip half-width (ESW), group size, population density, and population size are the common parameters. The ESW is defined as the distance from the line at which the expected number of animals detected beyond a certain distance is equal to the expected number of animals missed within that same distance from the line. ESW is apparently narrower after extrapolation in DISTANCE than in Kelker and can be mainly accounted to the subjective selection of the cutoff point *a*. Group size estimates are almost the same with approximately 4 individuals/group, while density and population size vary considerably between the two methods. The detection probability, which is denoted as the probability of observing an animal within a certain distance in a defined area, only applies for population extrapolation in DISTANCE. This parameter (100% detectability at 1.00) occurs as a function of the perpendicular distance of the detected animal from the transect, so it decreases as animals are detected further from the line. The detection probability of long-tailed macaques in PPSRNP is relatively high, with an average of 0.89 using group and individual count data. Furthermore, truncation of perpendicular distance data was done one-sidedly (right truncation) for both methods, although it was more subjective in the case of the Kelker method. All population parame-

Table 3. Mean values of meteorological parameters recorded during observations in PPSRNP (PAGASA, 2016)

MONTH	PRESSURE (mean sea level pressure, hPa)	TEMP (degC)	MEAN RELATIVE HUMIDITY (%)	RAINFALL (mm)	AVE. WIND SPEED (mps)	PREVAILING DIRECTION (degrees)	MEAN CLOUDINESS (Oktas)	MISCELLANEOUS WEATHER EVETNS WHICH OCCURRED ON SPECIFIC DATES					
								Smoke/ Haze/ Smaze	Fog	Rain/ Drizzle	Hail	Thunder storm	Lightning
March	1012.7	28.8	72	-	4	90	2	27, 30	-	-	-	-	-
April	1011.1	30.1	70	-	4	90	3	-	-	-	-	15	14, 15
May	1009.9	30.4	74	-	3	270	4	-	-	1,2	-	1,2	1,2

ters calculated via DISTANCE were modeled using the hazard-rate key function with simple polynomial adjustments since it yielded the lowest AIC value.

For the group count data, estimates of population density yielded 0.073 and 0.317 individuals/km^2 and population size resulted to 1596 and 689 individuals for DISTANCE and Kelker, respectively. Note that the area for which both methods extrapolated these estimates is the same (218.263 km^2), and that only the estimated half-width (ESW) differ among the parameters used to estimate population. It is possible that the parameter values calculated from the Kelker method are considerably underestimates. As per the National Academy of Sciences (1981), the Kelker method has the tendency to overestimate density because it underestimates the size of the area censused.

For the individual count data, the values calculated via DISTANCE and Kelker evidently resulted to over- and underestimates, respectively, with a total population size of around 5,700 individuals via DISTANCE, and 700 individuals via Kelker. Aside from estimating the perpendicular distance of the center of a group from the transect, each individual in the group was also treated independently and perpendicular distance for every reasonable discrete macaque was estimated as well. Clearly, however, this violates the fourth assumption which states that "detections must be independent events." The consequence of such violation is referred to by Buckland *et al.* (2015) as 'overdispersion,' where over-dispersed frequencies are apparent when plotted by distance interval in a histogram. In the present study, a little overdispersion of frequencies was indeed noticeable in 7.5-meter intervals, but not so much in 11.5-meter intervals. On the contrary, independently recording animals that occur in clusters may be a preferred option if clusters are so spread out that the location of the center is difficult to identify (Buckland *et al.*, 2015), which is actually the case for long-tailed macaques in PPSRNP.

In DISTANCE, density and group size estimates were based on the detection probability function with the lowest AIC values. Population modeling for *M. fascicularis* was determined using both group and individual count data which were truncated at the largest 5% of the observed distances. The hazard-rate key function with simple polynomial expansions provided best fit to the data (Figure 2). According to Buckland *et al.* (2015), the typical fit of detection function in a hazard-rate model gives a wider, flatter shoulder and is associated with better precision, a characteristic that is shown in Figure 2.

Density and group size estimates via the Kelker method were determined based on the distribution of detection distances in Figure 3. The cutoff point of effective strip width for the long-tailed macaque is 43 m and 47 m for group and individual count data, respectively.

In this study, population modeling through DISTANCE was considered to have generated relatively reliable estimates of population density and size. To begin with, the number of individual detections (n=143) recorded during fieldwork satisfied minimum requirements (>60-80 as per Buckland *et al.,* 2015) needed for reliable analysis, however, the corresponding number of group counts (n=38) did not. This issue with sample size in DISTANCE is compensated by the number of line transects (n=10) and the total sampling effort (n=40 km) (>20km as per Buckland *et al.,* 2015). On the other hand, because many observations are discarded in the Kelker method, a large number of detections is even more required (Marshall *et al.,* 2008) making fieldwork more demanding in a considerably large

Table 4. Population parameters calculated from three perpendicular distance methods for estimating density of group-living animals from line transects

METHOD	DATA ANALYZED	POPULATION PARAMETER								
		Encounter rate	ESW	Detection probability	Mean group size	Density estimates (groups/ km^2)	Density estimates (individuals / km^2)	Population size estimates	Data truncation	Model
DISTANCE	Group counts	0.21 (0.16 - 0.26)	57.2 m (40.4 m – 81.0 m)	0.94 (0.66 – 1.00)	3.62 (2.66 – 4.93)	0.018 (0.012- 0.027)	0.073 (0.044 – 0.121)	1596 (967 – 2633)	Right truncation (5% of the largest distances)	Hazard-rate with simple polynomial adjustments
	Individual counts	2.57 (1.59 – 4.14)	48.7 m (42.6 m – 55.6 m)	0.84 (0.74 – 0.96)	n/a	n/a	0.264 (0.161 – 0.432)	5756 (3516 – 9423)		
Kelker	Group counts	n/a	86 m	n/a	3.87	0.082	0.317	689	within cutoff point *a* = 43 m	n/a
	Individual counts	n/a	94 m	n/a	n/a	n/a	0.336	650	within cutoff point *a* = 47 m	n/a

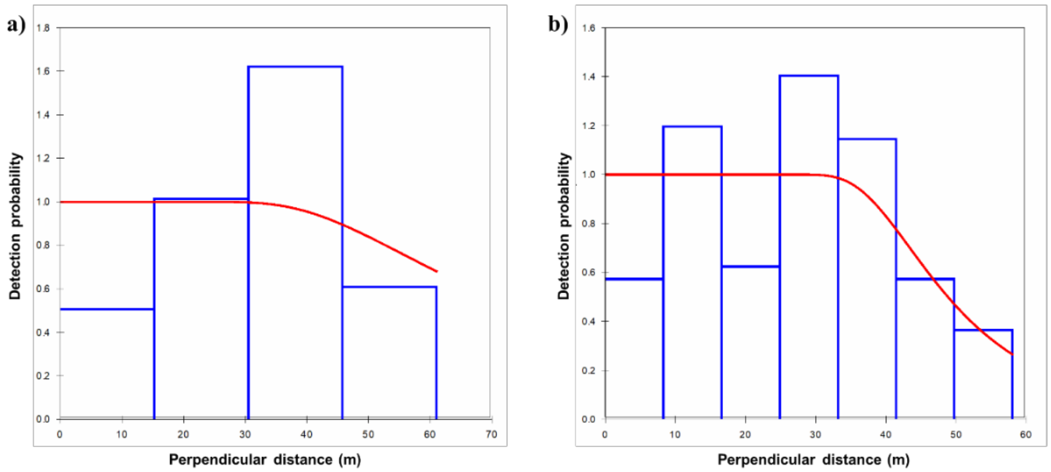

Fig. 2. Detection functions from DISTANCE for (a) group count data and (b) individual count data. Fit functions (hazard-rate with simple polynomial expansions) are represented by the red line.

study area such as the PPSRNP. The choice of truncation distance *a* in the Kelker method is also unquestionably subjective, uncertain, and influential and may thus yield strongly biased estimates of density (Buckland *et al.,* 2010).

However, it is possible that model selection based on the smallest AIC may be a source of bias in DISTANCE, as argued by Gonzalez *et al.* (2017) who reported that true detection functions with wide shoulders give up to 10% positive bias for line transect sampling. To generate unbiased estimates, Gonzalez *et al.* (2017) suggested increasing the sample size, ensuring adequate search effort at and close to zero distance, and using monotonicity constraints in analyzing count datasets. It is thus important to note, as is often the case of population surveys of forest-dwelling primates, that the estimates of density and abundance extrapolated in this study – regardless of the method of extrapolation – may be conservative over- or underestimates.

Due to the lack of baseline information on distribution and abundance estimates of macaques in the park, even more so in the Philippines, no inferences regarding population trend and the corresponding factors that influence it can be drawn locally. On the other hand, studies on long-tailed macaque populations (core species *M. fascicularis fascicularis*, and subspecies *M.f. aurea* and *M.f. karimondjiwae*) from neighboring Southeast Asian countries (e.g. Myanmar, Singapore, Indonesia, Thailand, and Malaysia) report densities that range from 7 to 120 individuals per square kilometer (Mi San & Hamada, 2011; Riley *et al.*, 2015; Yanuar *et al.*, 2009; Afendi *et al.*, 2011; Gumert *et al.*, 2012; Gumert *et al.*, 2013; Md-Zain *et al.*, 2010). These values are way higher than the densities calculated in the present study. Based on observations in the field, long-tailed macaques have a strong tendency to split into subgroups that forage and travel independently for hours during daytime; it is thus likely that the subgroups were counted as separate entities along line transects.

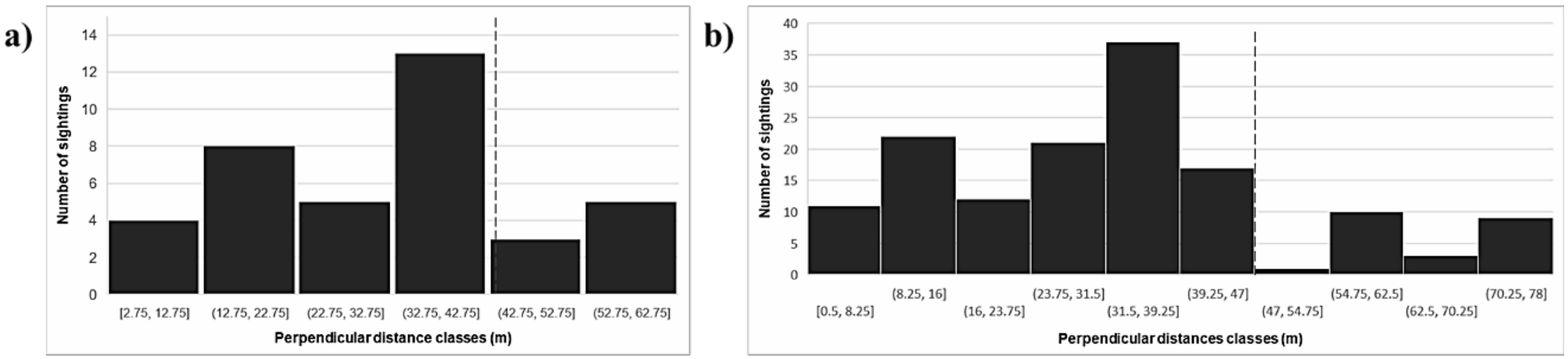

Fig. 3. Effective strip width diagram(s) via Kelker method using (a) group center and (b) individual perpendicular distances. Dotted lines demarcate the effective strip width within which detection probability is expected to be 1.0 (based on observations of maximum number of individuals' data)

This may account for the small mean group size calculated via Kelker and DISTANCE (Table 4) which are comparable to the known group size of long-tailed macaques observed in the wild. With regards to using perpendicular distances of group centers to extrapolate population densities, as long as long-tailed macaques are concerned, group size may be more appropriately referred to as 'subgroup' size in studies that utilize line transects and where census walks are conducted within the peak hours (0600-1000) of macaque activity in the morning. The term group size may thus apply to long-tailed macaques if the study design involves long-term observation of several focal groups within an area of interest.

Population estimates reported in earlier studies, however, are mostly based on direct counts (e.g. King's method, animal-to-observer distance; focal group sampling, tracking, etc.) (Mi San & Hamada, 2011; Riley *et al.,* 2015; Afendi *et al.,* 2011; Gumert *et al.,* 2012; Gumert *et al.,* 2013; Md-Zain *et al.,* 2010) rather than the use of randomly placed line transects for distance sampling (Yanuar *et al.*, 2009). Population assessments of primate populations, in general, view long-term monitoring as the most reliable, despite being time and cost intensive (National Research Council, 1981). However, with limited resources, population surveys that utilize line transects – this study included – have also proved to be efficient in terms of time and finances although this entails satisfying several assumptions.

The reliability of census data for population monitoring depends greatly on the ability of observers to meet method assumptions. The observer did not likely missed macaques over or near the transect during surveys (e.g. detection probability ≥ 0.89 within 53 m). Macaques spotted on trees (i.e. feeding on young leaves, grooming/playing) were conspicuous mainly because of their calls (i.e. kra, barks, coos) or movement through vegetation. In most detections, however, the macaques were observed to make several alarm calls before distances are even recorded, which suggests that they might have seen or heard our group before we detected them. These resonating alarm calls which are typically given off by a single macaque trigger nearby macaques to move away ('responsive movement') from a potential threat, which, in this case, are the observers.

According to Buckland *et al.* (2015), responsive movement (i.e. animals near the line move away from the observer before detection but remain in detection range) gives a tendency for the data to have excess detections at mid-distances, and too few detections at short distances. This effect is somehow evident in detection probability plots generated in CDS (Figure 2). The effect of responsive movement to detection functions is the tendency of the fitted model to average out the lack of detections near the line or point with the excess of detections at mid-distances. Apparently, for line-transect sampling, movement generates bias both in the count of animals and in the estimate of detection function, and these two sources of bias interact in a way that reduces overall bias (Buckland, 2015). Line transect data and the generated plots for detection probability show that responsive movement or avoidance undeniably occurred during data collection. Although observers moved slowly and quietly in surveys, most transects have thick leaf litter cover during the dry season; walking through dry leaves is thus a main source of unwanted background noise (Peres, 1999) and could have come off as a threat signal for long-tailed macaques near the transects.

With regards to the appropriateness of sampling effort and size, this study has satisfied the minimum requirements for reliable estimation of encounter rate and detection function. In DISTANCE, sampling effort is the length of the line multiplied by the number of visits (Buckland *et al.,* 2015). Buckland *et al.* (2001) also recommend a minimum of 10-20 replicate lines to allow reliable estimation of variance of encounter rate, without calling attention on the size of the study area; while reliable estimates of detection function require 60-80 detected animals. In the present study, ten line transects that are two kilometers each in length were established in the PPSRNP, whose area is approximately 21,826.26 hectares. The overall sampling effort was 40 kilometers, while line transect data yielded 143 detections of individual long-tailed macaques.

Other studies on tropical forest, diurnal primates report that the ideal length for transects should be 5-10 kilometers long (Ferrari *et al.*, 2010) or much longer trails without replication (Magnusson, 2001 as cited by Ferrari *et al.*, 2010). Coudrat *et al.* (2011) established shorter transects (1 km) which are visited more frequently (twice over ten days) during a month-long survey. In contrast, a primate survey conducted in Uganda (Plumptre and Cox, 2006) established eight four-kilometer transects which were walked every two weeks for a period of 3-4 months. Surveys of Amazonian primates by Peres (1999) used two long random transects (4-5 km) with at least 1 km interval, with a target sampling effort of 300 km for both transects (achieved by 2 independent observers walking both transects simultaneously for 17 days). Apparently, transect placement is inherently dependent upon the objectives of the survey (Peres, 1999) because the survey method, sampling design, intensity and frequency of sampling, and team capacity vary considerably among studies (Kuehl *et al.*, 2008 as cited in Campbell *et al.*, 2016). These studies also highlighted manifold threats to the species which include habitat loss and degradation, increasing conflict with human and domestic animal populations in both rural and urban landscapes, illegal wildlife trade (e.g. bushmeat consumption, being sold to exotic pet enthusiasts, etc.), as well as trapping and trade for pharmaceutical testing, research, and development (Mi San & Hamada, 2011; Riley *et al.*, 2015; Yanuar *et al.*, 2009; Afendi *et al.*, 2011; Gumert *et al.*, 2012; Gumert *et al.*, 2013; Md-Zain *et al.*, 2010; Eudey, 2008). This is why the long-tailed macaque, under IUCN's Red List, has been facing continuous population declines during the past two decades (Eudey, 2008) while the most important knowledge gap – reliable estimates of population and distribution of species and subspecies – are currently or yet to be addressed (Gumert, 2011).

Concluding Remarks

The results of this study suggest that line transect distance sampling is a relatively simple, rapid, and robust method in estimating the population and determining the distribution of long-tailed macaques within a given area. DISTANCE and the Kelker method are both reliable techniques in extrapolating density, mean group size, and population size. However, it is important to note that the vulnerability of the method lies to a wide range of bias which could be mainly accounted to violations in the assumptions of line transect sampling. Although the results in this study provide the first census data on long-tailed macaques in PPSRNP, further survey work is still needed to better refine these estimates. Nevertheless, long-tailed macaques at the PPSRNP are abundant and widespread, given that they are conspicuous during transect walks across different habitat types, despite certain anthropogenic disturbances observed within the park.

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REFERENCES

Aggimarangsee, N. (1992). Survey for semi-tame colonies of macaques in Thailand. Natural History Bulletin of the Siam Society. 40:103-166.

Altman, N.H., Brackett, B.G., Goy, R.B., Marriott, B.M., New, A.E., Senner, J.W., Eisenberg, J.F., Dittus, W.P.J., Fleming, T.H., Green, K., Struhsaker, T., & Thorington, R.W. (1981). Techniques for the study of primate population ecology. [Electronic copy]. National Academy Press. Washington, D.C. ISBN 0-309-03179-6.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Brochers, D.L., & Thomas, L. (2001). Introduction to Distance Sampling: Estimating abundance of biological populations. Oxford University Press, Inc. New York.

Buckland, S.T., Plumptre, A.J., Thomas, L., & Rexstad, E.A. (2010). Design and analysis of line transect survey for primates. International Journal of Primatology. 31 (5). Pp. 883-847. DOI: http://dx.doi.org/10.1007/s10764-010-9470-y

Buckland, S.T., Rexstad, E.A., Marques, T.A., & Oedekoven, C.S. (2015). Distance sampling: Methods and Applications [electronic copy]. Springer International Publishing. Switzerland. ISSN 2199-3203. DOI 10.1007/978-3-319-19219-2.

Campbell, D.J. (1968). Parasitic diseases of laboratory animals. Canad. Med. Ass. J. 98: 908-910.

Campbell, G., Head, J., Junker, J., & Nekaris, K.A.I. (2016). Primate abundance and distribution: background concepts and methods. In: Wich, S.A. and Marshall, A.J. An Introduction to Primate Conservation. 1st ed. Oxford. Oxford University Press. p. 79-110.

Coudrat, C.N.Z., Rogers, L.D., & Nekaris, K.A.I. (2011). Abundance of primates reveals Samkos Wildlife Sanctuary, Cardamon Mountains, Cambodia, as a priority area for conservation. Oryx. 45(3): 427-434. DOI: 10.1017/S0030605310001080.

Engelhardt, A. (1997). Impact of tourist contact on the competitive and social behavior of wild long-tailed macaques (Macaca fascicualris). MS Thesis. Berlin, Germany: Free University of Berlin.

Ferrari, S.F., Chagas, R.R.D., & Souza-Alves, J.P. (2010). Line transect surveying of arboreal monkeys: Problems of group size and spread in a highly fragmented landscape. American Journal of Primatology. 72: 1100-1107. DOI: 10.1002/ajp.20873.

Fittinghoff, N.A. & Lindburgh, D.G. (1980). Riverine refuging in East Bornean M. fascicularis. In The Macaques: Studies in Ecology, Behavior and Evolution, D.G. LINDBURGH (ed.). New York: Van Nostrand Reinhold. Pp.182-214.

Fooden, J. (1995). Systematic review of Southeast Asian long-tailed macaques, Macaca fascicularis (Raffles, [1821]). Zoology. (81). [Electronic copy]. Field Museum of Natural History. Chicago, Illinois.

Fooden, J. (1991). Systematic review of Philippine macaques (Primates, Cercopithecidae: Macaca fascicularis subspp.). Fieldiana: Zoology. 64. Field Museum of Natural History. Chicago, Illinois. ISSN 0015-0754.

Galvin, J. F. P., & Jones, C. D. (2009). The weather and climate of the tropics: Part 10–Tropical agriculture. Weather, 64(6), 156-161.

Gonzalez, R.P., Thomas, L., & Marquez, T.A. (2017). Estimation bias under model selection for distance sampling detection functions. Environmental and Ecological Statistics. 24(3): 399-414. Springer US. ISSN 1573-3009. https://doi.org/10.1007/s10651-017-0376-0.

Gumert, M. (2011). The common monkey of Southeast Asia: Long-tailed macaque populations, ethnophoresy, and their occurrence in human environments. Monkeys on the Edge: Ecology and Management of Long-tailed Macaques and their Interface with Humans. Cambridge University Press. ISBN 978-0-521-76433-9.

Hamilton, W.J. Iii & Watt,K.E.F. (1970). Refuging. Annual Review of Ecology, Evolution and Systematics. 1:263-286.

Fuentes, A. (2011). Monkeys on the edge: ecology and management of long-tailed macaques and their interface with humans (Vol. 60). Cambridge University Press.

Kurland, J.A. (1973). A natural history of Kra macaques (Macaca fascicularis, Raffles, 1821) at the Kutain reserve, Kalimantan, Timur, Indonesia. Primates. 14:245-262.

Mearns, E. A. (1905). Descriptions of new genera and species of mammals from the Philippine Islands. Proceedings of the United States National Museum. 28. pp. 425-460.

Malaivijitnond, S., Hamada, Y., Varavudhi, P., & Takenaka O. (2005). The current distribution and status of macaques in Thailand. The Natural History Journal of Chulalongkorn University. (Suppl. 1): 29-34.

Mallari, N.A.D., Collar, N.J., Lee, D.C., Mcgowan, P.J.K., Wilkinson, R., & Marsden, S.J. (2011). Population densities of understorey birds across a habitat gradient in Palawan, Philippines: implications for conservation. Oryx. 45 (2). pp. 234-242. DOI: 10.1017/S0030605310001031.

Mallari, N.A.D., Tabaranza, B.R., & Crosby, M.J. (2001). Key conservation sites in the Philippines. Haribon-BirdLife International and Bookmark Inc. Makati and Quezon City, Philippines.

Mallari, N. A. D. (2009). Maximising the value of ecological and socio-economic data in support of conservation planning for key understorey bird species in Palawan, Philippines (Doctoral dissertation, PhD Thesis, Manchester Metropolitan University).

Mallari, N. A. D., Rico, E. L., De Alban, J. D., Diesmos, A. C., Altamirano, R. A., Puna, N., ... & Monzon, A. (2013). Biodiversity baseline assessment in the REDD-Plus pilot and key biodiversity area in Mt. Nacolod, Southern Leyte. Manila: Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ).

Marshall, A.R., Lovett, J.C., & White, P.C. (2008). Selection of line-transect methods for estimating the density of group-living animals: Lessons from the primates. American Journal of Primatology. 70: pp. 1-11. DOI 10.1002/ajp.20516

Muehlenbein, M. (2015). Basics in human evolution. 1st ed. Academic Press.

National Research Council. (1981). Techniques for the study of primate population ecology. National Academies.

Ong, P. & Richardson, M. (2008). Macaca fascicularis ssp. philippensis. The IUCN Red List of Threatened Species. Version 2014.1. Retrieved 4 July 2014 from www.iucnredlist.org.

Peres, C. A. (1999). General guidelines for standardizing line-transect surveys of tropical forest primates. Neotropical primates, 7(1), 11-16.

Philippine Institute For Development Studies (PIDS). (2005). Basics on Philippine climatology. Economic Issue of the Day. 5(2).

Plumptre, A.J. & Cox, D. (2006). Counting primates for conservation: primate surveys in Uganda. Primates. 47: 65-73. DOI: 10.1007/s10329-005-0146-8.

Quantum-Gis Development Team (2018). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.

R Core Team. (2000). R language definition. Vienna, Austria: R foundation for statistical computing.

RICHARD, A.F., GOLDSTEIN, S.J., & Dewar, R.E. (1989). Weed macaques: the evolutionary implications of macaque feeding ecology. International Journal of Primatology. 10:569-594. Retrieved 24 March 2018 from DOI 10.1007/BF02739365.

Sha, J., Humert, M.D., Lee, B.P.Y-H., Et Al., (2009a). Status of the long-tailed macaque Macaca fascicularis in Singapore and implications for management. Biodiversity and Conservation. 18:2909-2926.

Sha, J., Gumert, M.D., Lee, B.P.Y-H., et al., (2009b). Macaque-human interactions and the societal perceptions of macaques in Singapore. American Journal of Primatology. 71:825-839.

Sussman, R. W., & Tattersall, I. (1981). Behavior and ecology of Macaca fascicularis in Mauritius: A preliminary study. Primates, 22(2), 192-205.

Sussman, R. W., & Tattersall, I. (1986). Distribution, abundance, and putative ecological strategy of Macaca fascicularis on the island of Mauritius, southwestern Indian Ocean. Folia primatologica, 46(1), 28-43.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B., & Marques, T.A. (2006). Distance 5.0 Release 2. Research Unit for Wildlife Population Assessment. University of St. Andrews, United Kingdom.

Thomas, L., S.T. Buckland, E.A. Rexstad, J. L. Laake, S. Strindberg, S. L. Hedley, J. R.B. Bishop, T. A. Marques, & K. P. Burnham. (2010). Distance software: design and analysis of distance sampling surveys for estimating population size. Journal of Applied Ecology 47: 5-14. DOI: 10.1111/j.1365-2664.2009.01737.x

Wheatley, B.P. (1978). Foraging pattern in a group of long-tailed macaques in Kalimantan Timur, Indonesia. In Recent Advances in Primatology, vol1: Behavior, D.J. CHIVERS & J. HERBERT (eds). New York: Academic Press. pp.347-349.

Wheatley B.P. (1980). Feeding and ranging of East Bornean Macaca fascicularis. In The Macaques: Studies in Ecology, Behavior and Evolution. D.G. LINDBURGH (ed.), New York: Van Norstrand. pp.215-246.

Wheatley, B.P. (1982). Energetics of foraging in Macaca fascicularis and Ponao pvamaeus and a selective advantage of large body size in the orang-utan. Primates. 23:348-363.

Whitesides, G.H., Oates, J.F., Green, S.M., & Kluberdanz, R.P. (1988). Estimating primate densities from transects in a West African rain forest: A comparison of techniques. Journal of Animal Ecology. 57 (2). pp. 345-367. DOI: 10.2307/4910.

Wilson, C.C., & Wilson, W.L. (1975). The influence of selective logging on primates and some other animals in East Kalimantan. Folia Primatologica, 23(4), 245-274.

Van Schaik, C.P., Van Amrerongen, A., & Van Noordwijk, M.A. (1996). Riverine refuging by wild Sumatran long-tailed macaques (Macaca fascicularis). In Evolution and Ecology of Macaque Societies. J.E. FA & D.G. LINDBURGH (eds.). Cambridge University Press pp. 160-181.