

Results of a nationwide census of the long-tailed macaque (*Macaca fascicularis*) population of Singapore

Crystal M. Riley^{1,2*}, Srikantan L. Jayasri^{2,3} & Michael D. Gumert²

Abstract. Long-tailed macaques (*Macaca fascicularis*) are known for their ability to thrive in a wide variety of habitats, including urban areas. Singapore is an island city-state that has experienced rapid deforestation and urbanisation over the past several decades. These processes have led to the loss of most of Singapore's large mammalian species, but long-tailed macaques still live on the island. We conducted a census of long-tailed macaques between 2011 and 2012 to determine the current status of Singapore's macaque population. We surveyed forest edges, counted groups, and classified the age and sex of all individuals. We estimated the macaque population to be 1810–2166 individuals distributed among 92 groups, and a density averaging 6.86 individuals per km² (range: 0.89–33.63 across six zones) in areas with macaques. We found no evidence of overpopulation. Rather, the population characteristics mirror those of non-provisioned, wild long-tailed macaque populations. However, the interpretation of our results is limited by the fact that we did not have access to records documenting the number of macaques culled in Singapore before and during this census. Without accurate culling records, it is not possible to assess what shapes the current population structure, and thus research on the past effects of culling is needed.

Key words. Singapore, long-tailed macaques, synanthropy, population census

INTRODUCTION

Monitoring wildlife populations is important for successful management. Management officials devise management strategies based upon the results of studies examining the status and distribution of species (Dice, 1938). Wildlife management plans are particularly important when the species of concern is one that shares a habitat with humans. In these situations, the mitigation of human-wildlife conflict must also be considered. One species well known for such conflict is the long-tailed macaque (*Macaca fascicularis*). Close interfaces between humans and long-tailed macaques are driven in part by these macaques' ability to thrive in diverse habitats, particularly disturbed habitats such as forest edges and human-inhabited areas (Gumert, 2011).

In Singapore, high human population density (7257 people per km² in 2012; SingStat, 2012) and limited space (land area of 714 km² as of 2012) bring people into close proximity with macaques. Singapore has lost much of its original biodiversity as a result of deforestation that began 170 years ago, and eventually gave way to urbanisation that continues today (Corlett, 1992). The highly urbanised island has patches

of protected forest, primarily in the Central Catchment Nature Reserves (CCNR) and Bukit Timah Nature Reserve (BTNR), which together comprise 3043 hectares, or 4.1% of Singapore's land area (National Parks Board, 2009). Conflict situations common elsewhere in SE Asia are absent in Singapore. There are no monkey temples, crop raiding is not a significant issue, and feeding monkeys is illegal, which discourages, but does not eliminate, people from feeding macaques. However, macaques' close contact with people does lead to problems such as food theft, garbage raiding, property damage, and, on rare occasions, macaques injuring people (Sha et al., 2009a; Feng, 2011).

The National Parks Board of Singapore (NParks) received an increase in macaque complaints in recent years, especially from 2007 to 2011. Public complaints range from reports of property damage and road kill incidents to people reporting macaque sightings. As macaque complaints in Singapore increased, the media has more frequently covered macaque issues (Fuentes et al., 2008; Khew, 2014). For example, Sha et al. (2009a) listed 47 macaque-related headlines from Singaporean newspapers between 2004 and 2008. Wildlife authorities have also increased attention to the rising complaints. For example, in August 2012, the Agri-Food and Veterinary Authority (AVA) opened a 24-hr hotline for receiving wildlife complaints (Feng, 2013), which had a major focus on macaques. Also in response to complaints, NParks acted to better understand the trends in Singapore's macaque population, and initiated our study after having received a 30% increase in macaque complaints in 2010 (611 in 2009 and 792 in 2010) (Gunasingham, 2011). The goal was to examine the macaque population and whether it had increased in size.

¹Department of Anthropology, Washington University in St. Louis, St. Louis, MO; Email: crystalmriley@wustl.edu (*corresponding author)

²Division of Psychology, School of Humanities and Social Sciences, Nanyang Technological University, Singapore; Email: gumert@ntu.edu.sg (MDG)

³Central Nature Reserves Branch, Conservation Division, National Parks Board, Singapore

METHODS

Incomplete efforts to monitor Singapore's macaques have been made in the past. First, in 1986, the Malayan Nature Society reported the total population on Singapore's main island was unlikely to exceed 1000 macaques (Lucas, 1995). However, the report did not include any methods, and thus was unclear how the estimate was generated. A few years later, Teo & Rajathurai (1997) conducted a survey and estimated the CCNR population to be 850 macaques in 34 groups, even though they reported 1415 observations of macaques over four years. A census in 2004, by Agoramoorthy & Hsu (2006), included more land area beyond the CCNR, which included BTNR, Rifle Range, and Mandai area; however, it excluded other areas with macaques such as offshore islands, Admiralty Park, and Woodlands Waterfront. In this census, they estimated the total population to be 649 individuals distributed among 32 social units, which was 24% less than the 1997 estimate; however, similar to other censuses, their brief report provides no explanation for how they came to the estimate. Taken together, none of the early reports were complete nor covered the entire country, and thus likely underestimated total population size. Furthermore, none of these reports provided population densities or distribution maps. These problems make the utility of these past estimates limited for understanding macaque population trends over time.

In 2007, Sha et al. (2009b) conducted the first complete, nationwide census of long-tailed macaques. Up to that date, it was the most reliable measure of the macaque population made in Singapore's history. Their survey estimated the macaque population was between 1218–1454 individuals in 71–112 groups. The population consisted of 53% immature individuals (i.e., adolescents, juveniles, and infants) and 47% adults. There were 0.44 infants per female, and 0.63 adult males per adult female. Macaque density was 5.22 ind km⁻² across all areas that contained macaques, and 28.2 ind km⁻² in the nature reserve areas. Lastly, during 2007, slightly over 200 macaques were recorded as culled, and 400–450 were recorded culled in total during the previous 5 years (2002–2006), indicating this population census was conducted on a population heavily affected by culling (Sha et al., 2009b).

Following Sha et al. (2009b) by five years, we conducted the second nationwide census for Singapore macaques in 2012. We investigated population characteristics of long-tailed macaques in Singapore, including size, distribution, density, and age-sex breakdown of the population. We compared our results to populations of long-tailed macaques in both provisioned and wild setting across their range to assess whether Singapore's population was overpopulated. Furthermore, we made an attempt to identify trends in the Singaporean macaque population over time by comparing our results to the 2007 census. We end by discussing the differences in the methods used and conditions between the Sha et al. (2009b) census and our own. We also discuss the lack of culling data in the time periods surrounding our study, and how culling might affect census counts.

Study area. Singapore is an island city-state at the southern tip of the Malay Peninsula. The country of Singapore includes a larger main island and more than 60 smaller offshore islands (SingStat, 2012). Most of the smaller islands are uninhabited and do not sustain large mammalian wildlife. Macaques have been observed on the main island and some of the larger offshore islands during previous censuses (Sha et al., 2009b). For this census, we used the six survey regions used by Sha et al. (2009b) (Fig. 1): 1) Bukit Timah, 2) MacRitchie, 3) Old Upper Thompson, 4) Mandai, 5) Islands, and 6) Other. The Other region encompassed any area not included in the first five regions that contained macaques. MacRitchie and Old Upper Thompson together made up the CCNR.

Selection of survey areas. To identify areas that might contain macaques, we compiled information from the previous census (Sha et al., 2009b), media reports (from The Straits Times, The Sunday Times, The New Paper, and Asia One), posts in online forums (e.g., Facebook and STOMP, which is a Singaporean citizen-journalism website), and a list of macaque complaints from NParks. The complaint list contained general locations of macaque issues reported by citizens between December 2010 and July 2012. We also examined a map of Singapore and added to our list of places to survey any forested areas not already identified. We asked members of the public (see below) about when and where they saw macaques, and if they mentioned places that we did not already intend to survey, we added those places to our list.

Once we compiled the list of survey locations, we began visiting each location, with the exception of Ministry of Defense (MINDEF) land, where the military conducts training exercises, including live firing of weapons. We were not granted permission to access or receive information about those sensitive areas. Without being able to survey MINDEF areas in the present survey, we just carried over the results of the previous census (Sha et al., 2009b), during which the government researchers were granted conditional access to some MINDEF land or were provided macaque estimates from MINDEF staff. Therefore, the estimates we used for the MINDEF areas were the figures from the 2007 survey.

Census methods. Data were collected over 150 days in the field between October 2011 and November 2012. Researchers had 535 contact hours with macaques, with additional time spent searching for macaques. In standard primatological censuses, each social unit is encountered and counted, and then researchers move on (Ross & Reeve, 2003). In our case, a pair of researchers (CR & SJ) each conducted their own multiple counts of every social unit encountered to achieve high accuracy. We spent an average of seven hours and 45 minutes with each social unit, typically over multiple days. During follows, we obtained accurate individual counts, assessed the age/sex distribution of individuals, and collected scan samples on behavior for other studies. It was possible to spend hours with social units because groups were sufficiently habituated to humans and did not flee; however, there were

five social units with which we spent less than an hour, due to them being unhabituated and fleeing from us.

Long-tailed macaques prefer forest edges (Gumert et al., 2011); therefore, when surveying a location, we began by walking edges in and around the area, except where access was prohibited (i.e., restricted and private land). Edges included designated outer boundaries of a park (e.g., the boundary of BTNR), as well as ecological edges within the region (e.g., trails through the forest, shorelines, roads). Our method of walking edges to survey a primate population differed from standard transect methods (Ross & Reeve, 2003), and did not involve as much coverage of the deep interior of the forest. However, Singapore's small forest patches and the presence of trails through the patches provided adequate access for observing macaques. We also did not use transects because it is a method for obtaining sample counts to extrapolate a population size estimate to a larger area. Our method attempted to count each individual in the population directly, which was feasible given the small population size and small area to cover. Similar full count methods were used for surveying Karimunjawan long-tailed macaques (*M. f. karimondjiwae*) on Karimunjawa Island, in Indonesia (Afendi et al., 2011), common long-tailed macaques (*M. f. fascicularis*) in parts of Tanjung Puting National Park in Kalimantan, Indonesia (Gumert et al., 2012), and Burmese long-tailed macaques (*M. f. aurea*) on Piak Nam Yai Island, in Ranong, Thailand (Gumert et al., 2013).

If we did not find macaques in an area we surveyed, we spoke with people in the area about whether or not they ever spotted monkeys. We wanted to speak with people familiar with the area, so we sought out, in order of preference, NParks staff, other employees (e.g., security guards, cleaners), residents, and park visitors. We asked when, where, and how many macaques they typically saw, and then we returned another day to survey the area, preferring to return at the time and place people reported seeing macaques (e.g., "early afternoon near the bridge"). It took up to six trips to a location to verify the presence of macaques. We were able to verify nine public reports in locations where we did not initially see macaques (e.g., Yishun Park; see Table 1). After a maximum of eight trips, if we had not found macaques where locals reported having seen them, we included the estimates in our records as "public reports." Public reports were helpful in identifying places that required further investigation. However, most of the people making reports, with the exception of NParks staff, did not have experience counting wild animals. Therefore, they were likely to provide overestimates, which have been found to be a common bias for public reports of macaque group sizes (Malaivijitnond et al., 2011). Due to possible inaccuracy and bias, we treated public reports with less confidence than our own survey counts, and did not include them into our minimum population estimate. We excluded reports older than six months.

As we searched for macaques, a GPS device (Garmin GPSMAP 62sc) recorded our location every 30 seconds to mark our survey paths. When macaques were sighted, we made a waypoint of our location, which served as the

starting point of our follow. From that starting point, our 30-second interval tracking record allowed us to map the ranging pattern of the macaques we were following. If the macaques stopped to sleep for the night, we marked the location of their roost. If we lost sight of the macaques or left them for any reason, we marked our location at that point to denote the end of the recorded range. Ranging data was used to ensure that we did not double-count a single group in different parts of its home range.

Counting and classifying macaques: Upon first encountering a social unit, both researchers counted them and scored the age class (i.e., adult, adolescent, juvenile, or infant) and sex, if discernible, of each individual. We determined age class by following rules based on descriptions from Fooden (1995). For example, a female was classified as a full adult if she had elongated nipples indicating that she had previously given birth, and a young macaque was classified as an infant if it retained black fur from its natal coat. We categorised social units into two types: groups (two or more macaques) and single animals. We further distinguished between multi-male/multi-female groups and all-male groups.

We did counts repeatedly for the first one to three hours after encountering a social unit. After each researcher began to achieve the same count consistently, we moved on to counting every 30 minutes as we followed the social unit, doing additional ad libitum counts if a good opportunity presented itself (e.g., all macaques approached a human food source). We entered count data into an Excel spreadsheet on a Psion Workabout Pro handheld computer.

For each count, we rated our confidence in the count as high, medium, or low. Confidence scores were a subjective assessment of our certainty that all macaques in the social unit were visible and counted, and were affected by the amount of time spent with the unit and the conditions of observation, including weather, forest coverage, and the macaques' activity. For instance, a count of a group that we observed for 30 minutes in dense forest on a rainy day would be low confidence, whereas a group we observed for 10 hours in a variety of conditions would be high confidence.

In addition to scored data, we used photographs to identify individuals in each group. We photographed all adults, and any immature macaques with unique identifying characteristics (e.g., a distinct scar). Individual identification was used in our study to assist counting and provided a photographic count of individuals by which to compare our field count. We used this method to ensure that we did not repeatedly count individuals, or repeatedly count a single social unit encountered in more than one area.

We collected behavioral scan samples (Altmann, 1974) every 30 minutes while with each social unit, using Noldus Observer XT software on a Psion Workabout Pro. We confirmed group counts by comparing the numbers and age/sex classes obtained during scan samples with those obtained during counts. Discrepancies indicated that we needed to conduct additional counts to ensure accuracy.

Scan samples also provided information on the amount of human feeding, including both direct human feeding and indirect access to human food (e.g., food foraged from trash bins), for each social unit and for the population overall. The results of our behavioral data collection are covered in Riley et al. (in press).

Analyses: We attempted to account for error in our counting by generating a range for our population estimate. First we calculated the minimum estimate, which was the sum of our physical counts in 2012, and the 2007 estimates from MINDEF land. Secondly, we made a best, or most likely, estimate by adding public reports to the minimum estimate. Lastly, we calculated a maximum estimate, using corrections discussed below.

Maximum estimates for primate populations are often calculated by extrapolating a density estimate to an entire forested area (Ross & Reeve, 2003). Although that method can be practical for some forest-dwelling primates, it is not appropriate for long-tailed macaques for two reasons. First, long-tailed macaques prefer forest edges and are not evenly distributed in a forest, so applying a density estimate uniformly across the forest would lead to a major overestimation of density. Second, the method of applying a density estimate across a larger region is typically used to compensate for not having surveyed an area. In our study,

we attempted to make a head-count of the entire population. We therefore only needed to make estimations for the potential error in our counting, but not for extrapolating to un-surveyed regions.

We used our high-confidence counts of group sizes as a correction tool for estimating maximum population size. To do this, we corrected all low and medium-confidence group counts to the mean from high-confidence counts. Two high-confidence correction means were used because group sizes differed between regions. We made a correction mean for the core area groups (i.e., MacRitchie, BTNR, Old Upper Thompson, and Mandai regions), and a second correction mean for non-core area groups (e.g., Island and Other regions). If a low or medium-confidence group count happened to be higher than the mean high-confidence group count for their region, we always corrected towards the larger count. We did not replace low and medium-confidence estimates that were higher than the correction means because we were correcting for under-counting not over-counting, the latter being less likely. That is, it was much more likely to overlook macaques that were not visible, than to mistakenly count “phantom” macaques.

We calculated and examined variation in population density and other population characteristics across the six regions (Fig. 1), which contained a total area of 278.28 km². We

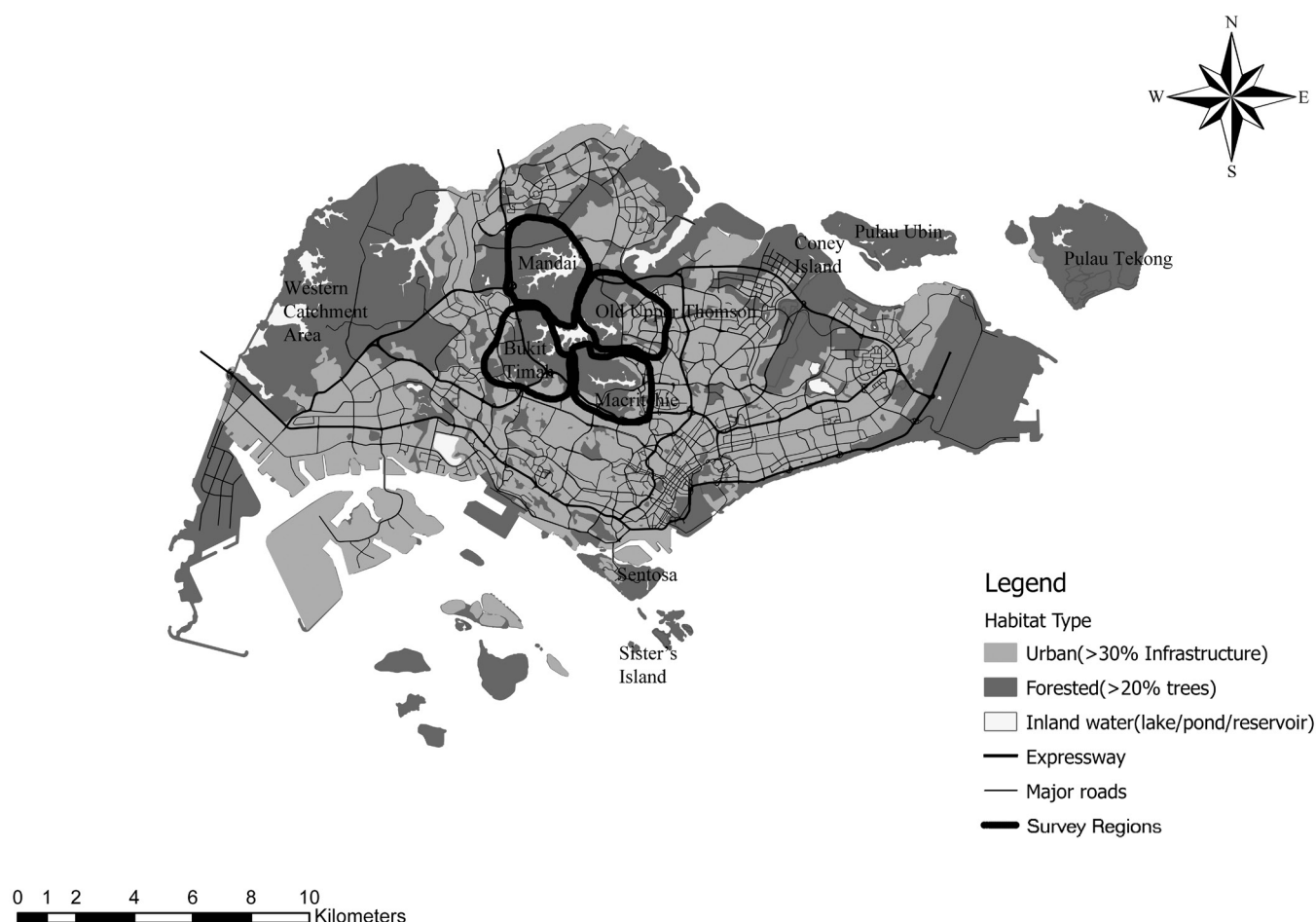


Fig. 1. The four core zones defined for the census are circled in black, Mandai, Old Upper Thompson, Bukit Timah, and MacRitchie. The Islands zone consisted of all the offshore islands that are labeled on the map, Ubin, Tekong, Sentosa, Coney, and Sisters. The Other zone was any area not included in the other five regions that contained macaques.

also calculated density for the core area, which were the four regions where the majority of the macaque population was concentrated. Since group characteristics can vary depending on habitat and level of human overlap (Aggimarangsee, 1992; Fooden, 1995), we examined group sizes and the ratios of adult males to adult females, infants to adult females, and immature to adult macaques to see how those ratios compared to other populations, especially populations living in environments less disturbed by people. We also conducted a t-test to see whether groups that accessed human food systematically differed in size from groups that did not access human food. All statistical analyses were conducted using IBM SPSS Statistics version 19.0, 2010, Armonk, NY. Alpha was set at 0.05 unless otherwise noted.

RESULTS

Population size. We physically counted 1626 macaques in 69 social units on mainland Singapore and four offshore islands (Table 1). The count excluded areas to which we did not have access (i.e., MINDEF land). The macaques we counted were distributed among 66 multi-male-multi-female groups (95.7% of social units; 99.8% of individuals); one all-male group (1.4% of social units; 0.1% of individuals); and two lone males (2.9% of social units; 0.1% of individuals). We calculated a mean (\pm SD) of 24.2 ± 9.85 macaques per group from 1624 macaques in 67 groups.

In addition to our physical count, we had to account for MINDEF and public reports. In MINDEF areas, we used Sha et al.'s (2009b) count from 2007 of 184 macaques, which was distributed among 13 groups (182 macaques) and two single animals (Table 2). We excluded two groups counted in 2007 at MINDEF ($N = 23$ and $N = 15$) because we counted groups of comparable size ($N = 21$ and $N = 14$) in areas adjacent to MINDEF land where these groups were in 2007. We thus considered them the same groups. The mean (\pm SD) group size for the 13 MINDEF groups was 14.0 ± 8.78 macaques. Combining MINDEF groups and 2012 survey groups resulted in a mean group size of 22.58 ± 10.36 macaques, $N = 80$. All MINDEF social units were rated as low confidence, because we did not count them directly in 2012. Unverified public reports of macaques amounted to an additional 99 macaques distributed among 12 groups (67 macaques) and 32 single animals (Table 3).

Using these counts, we calculated the best estimate of the population to be 1909 individuals. This figure included our physical count of 1626, plus the 2007 MINDEF count of 184, plus the 99 macaques from public reports. However, since the public reports were not verifiable and thus could be inaccurate or biased, we also calculated a minimum count of 1810, which excluded the public reports. This minimum count was considered the lowest possible size the population could be. Public reports were from our discussions with

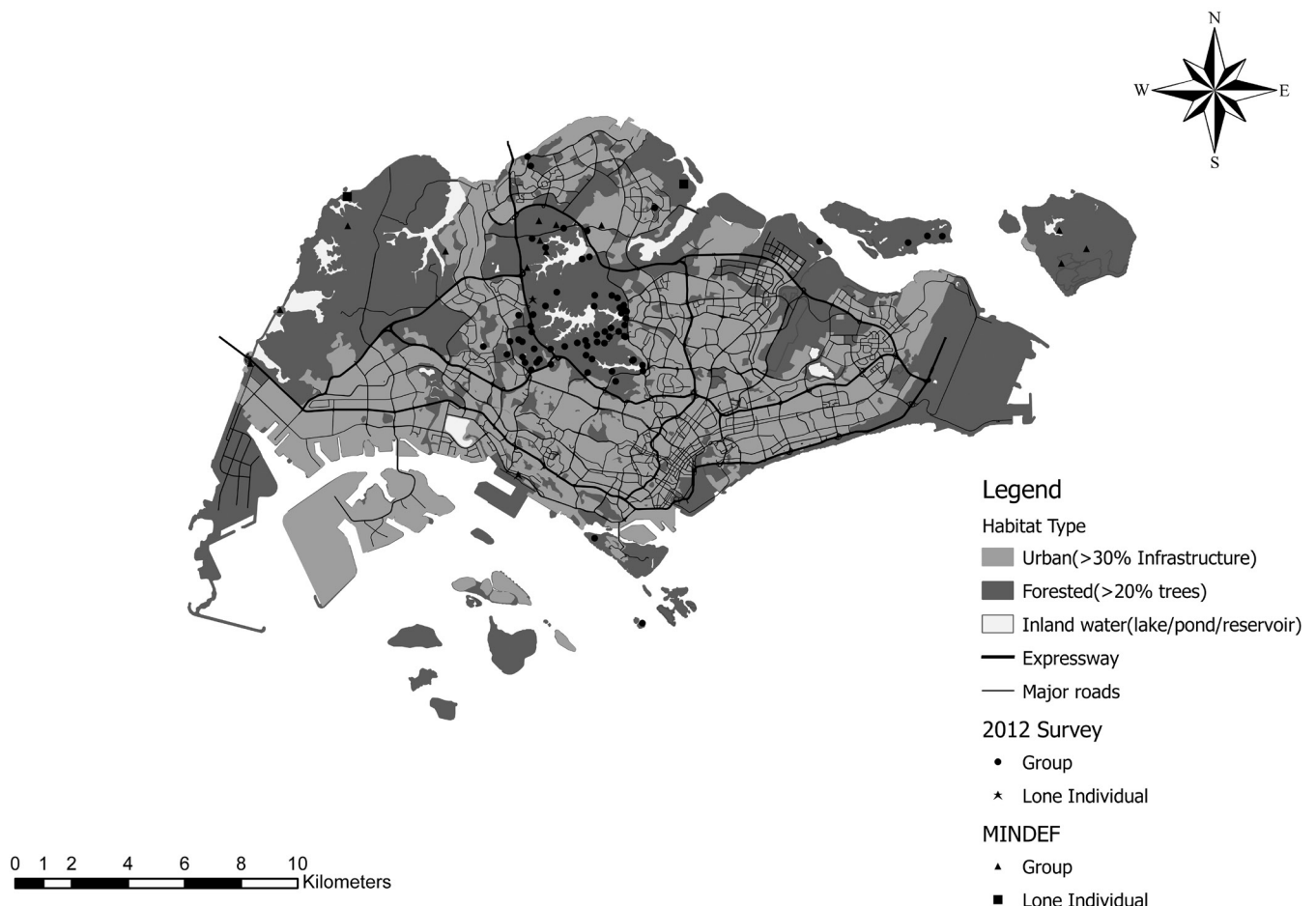


Fig. 2. The distribution of macaques in Singapore in 2012, which includes the 2012 census observations and 2007 MINDEF survey.

Table 1. Summary of the characteristics of all social units counted in 2012. Single animals italicised.

Region	Social Unit ID	2012 Count	Adult ♂	Adult ♀	Adol/ Juv	Infant	Im-mature	Adult ♂:♀	Adult: Immature
Bukit Timah	BB01	38	6	12	16	4	20	0.50	0.90
	BT01	47	7	16	19	5	24	0.44	0.96
	BT02	29	4	11	9	5	14	0.36	1.07
	BT03	43	6	14	12	11	23	0.43	0.87
	BT04	20	4	6	8	2	10	0.67	1.00
	BT05	38	5	12	17	4	21	0.42	0.81
	BT06	18	2	5	11	0	11	0.40	0.64
	BT07	3	0	1	2	0	2	0.00	0.50
	CA01	15	2	7	6	0	6	0.29	1.50
	CA02	26	4	5	17	0	17	0.80	0.53
	DF01	26	3	6	15	2	17	0.50	0.53
	RR01	21	2	7	8	4	12	0.29	0.75
	RR02	32	4	10	15	3	18	0.40	0.78
	RR03	40	5	13	14	8	22	0.38	0.82
	RR04	35	4	11	13	7	20	0.36	0.75
	RR05	31	6	10	14	1	15	0.60	1.07
	ZP01	21	2	5	12	2	14	0.40	0.50
	MacRitchie	BC01	27	3	7	16	1	17	0.43
IC01		28	7	9	10	2	12	0.78	1.33
IC02		22	3	9	8	2	10	0.33	1.20
IC03		26	5	4	15	2	17	1.25	0.53
IC04		40	6	10	24	0	24	0.60	0.67
MR01		26	4	7	12	3	15	0.57	0.73
MR02		48	7	11	28	2	30	0.64	0.60
MR03		26	5	8	11	2	13	0.63	1.00
MR04		28	5	5	16	2	18	1.00	0.56
MR05		26	6	6	12	2	14	1.00	0.86
MR06		22	4	6	10	2	12	0.67	0.83
MR07		16	2	6	5	3	8	0.33	1.00
MR08		23	3	4	12	4	16	0.75	0.44
MR09		22	2	8	10	2	12	0.25	0.83
MR10		11	2	4	4	1	4	0.50	1.50
MR11		18	1	2	14	1	15	0.50	0.20
MR12		16	2	4	9	1	10	0.50	0.60
MR13		8	2	3	3	0	3	0.67	1.67
MR14		20	6	4	8	2	10	1.50	1.00
MR15	15	2	5	6	2	8	0.40	0.88	
SI01	33	4	9	15	5	20	0.44	0.65	
Old Upper Thompson	IC05	26	3	10	5	8	13	0.30	1.00
	LP01	25	3	6	14	2	16	0.50	0.56
	LP02	27	4	6	14	3	17	0.67	0.59
	LP03	19	4	5	8	2	10	0.80	0.90
	LP04	25	3	7	13	2	15	0.43	0.67
	OT01	22	4	4	13	1	14	1.00	0.57
	OT02	25	4	9	10	2	12	0.44	1.08
	OT03	32	7	9	14	2	16	0.78	1.00
	OT04	35	3	12	16	4	20	0.25	0.75
	UP01	27	6	9	8	4	12	0.67	1.25
	UP02	24	5	10	8	1	9	0.50	1.67
Mandai	MD01	34	5	9	17	3	20	0.56	0.70
	MD02	36	3	10	15	8	23	0.30	0.57
	ML01	21	3	4	13	1	14	0.75	0.50
	ML02	21	4	6	9	2	11	0.67	0.91
	US01	31	3	12	10	6	16	0.25	0.94
	US02	38	6	10	19	3	22	0.60	0.73

Region	Social Unit ID	2012 Count	Adult ♂	Adult ♀	Adol/ Juv	Infant	Im-mature	Adult ♂:♀	Adult: Immature
Islands	CI01	17	2	3	12	0	12	0.67	0.42
	PU01	18	4	5	7	2	9	0.80	1.00
	PU02	17	5	2	10	0	10	2.50	0.70
	PU03	15	4	4	5	2	7	1.00	1.14
	SS01	17	4	3	10	0	10	1.33	0.70
	ST01	7	2	1	4	0	4	2.00	0.75
Other	AP01	26	4	8	12	2	14	0.50	0.86
	BB02	2	2	0	0	0	0	--	--
	CA03	16	2	5	6	3	9	0.40	0.78
	CA04	17	2	3	11	1	12	0.67	0.42
	<i>NU01</i>	<i>1</i>	<i>0</i>	<i>0</i>	<i>1</i>	<i>0</i>	<i>0</i>	--	--
	<i>WT01</i>	<i>1</i>	<i>1</i>	<i>0</i>	<i>0</i>	<i>0</i>	<i>0</i>	--	--
	WW01	15	3	6	4	2	6	0.50	1.50
	YP01	5	1	1	3	0	3	1.00	0.67
67 groups	1624	252	461	746	165	911	0.55	0.78	
<i>2 single animals</i>	<i>2</i>	<i>1</i>	<i>0</i>	<i>1</i>	<i>0</i>	<i>1</i>	--	--	
Total	1626	253	461	747	165	912	0.55	0.78	

Table 2. Estimates of macaques on MINDEF land that were carried over from Sha et al. (2009b). MINDEF provided Sha et al. (2009b) a range estimate for these numbers. We have used the mean of the range provided. Single animals are italicised.

Location	Count
Asrama	20
Khatib Bongsu	1
Lada Hitam	10
Lorong Kebasi	13
Mandai Track 15 Group1	10
Mandai Track 15 Group2	10
Pulau Tekong Reservoir	3
Pulau Tekong Highway	33
Pulau Tekong Grenade Range	22
Tagore	8*
Ulu Sembawang Forest	10
Western Catchment Poyan	15
Western Catchment Tengah	1
Western Catchment Track 13	25
Western Catchment Sarimbun	3*
13 groups	182
<i>2 single animals</i>	<i>2</i>
Total	184

52 people in 25 locations. In 12 of those locations, people reported no macaques in the past six months. In six locations, people reported recent macaque sightings that were later confirmed by us visually. In seven locations, we could not confirm recent macaque sightings (Table 3).

We performed corrections to some group counts to account for potentially uncounted animals and generated a maximum estimate from these corrections. Of the 67 groups we observed, 23 (34.3%) were judged as high confidence, 35 (52.3%) as medium confidence, and 9 (13.4%) as low confidence. In addition, all 13 groups from the 2007 MINDEF survey were considered low confidence and were corrected. We used the mean from high-confidence counts to correct all 35 medium and 22 low-confidence group counts. We found that the core area had a higher mean group size than the rest of Singapore (independent samples t-test: $t(65) = -4.331$, $P < 0.001$, two-tailed); therefore, we calculated a high-confidence mean for the core area ($N = 19$, $M = 30.05 \pm 10.59$), and a second high-confidence mean, for everywhere else ($N = 4$, $M = 9.75 \pm 7.365$). We then raised all medium and low-confidence counts lower than this mean, to the high-confidence mean for the region of the group (i.e., core or other). This correction resulted in adding 257 macaques to our estimate of 1909, producing a maximum population estimate of 2166 macaques, which we considered to be the largest possible population size in 2012. From all counts and estimates, we concluded the macaque population for mainland Singapore and its offshore islands was between 1810 and 2166 individuals, with a best estimate of 1909 macaques.

Population characteristics. Data on age-sex composition of groups were only available for social units directly counted during the survey. Of 1626 macaques counted, 714 (43.9%) were adults (253 males; 461 females), 165 (10.2%) were infants, 101 were adolescents (6.2%), and 646 were juveniles (39.7%). Immature macaques accounted for 56% of the population, with a ratio of 1.28 immature individuals per adult. We did not find a significant relationship between group size and the ratio of immature to adult individuals (Pearson Correlation: $r(65) = -0.088$, $P = 0.484$). The ratio of infants ($N = 165$) per adult female ($N = 461$) was 0.36. There was a statistically significant relationship between group size and ratio of infants to adult females (Pearson Correlation: $r(66) = 0.350$, $P = 0.004$). We calculated a sex ratio of 1.85 adult females per adult male, or 0.54 adult males per adult female. The male to female sex ratio of island groups was nearly two times higher ($M = 1.38 \pm SD = 0.72$, $N = 6$) than the ratio of non-island groups ($M = 0.56 \pm SD = 0.26$, $N = 60$), (independent samples t-test: $t(5.13) = -2.77$, $P = 0.038$, two-tailed, equal variances not assumed). There was a significant correlation between the size of the group and adult female to male sex ratio, $r(66) = -0.25$, $P = 0.041$. Lastly, social units observed feeding on human food during scan samples had significantly larger group sizes ($M = 28.27 \pm SD = 11.50$) than social units not observed feeding on human food ($M = 21.36 \pm SD = 9.28$), $t(67) = 2.67$, $P = 0.010$.

Population distribution. We calculated densities from the minimum population estimate, which were the counts from the 2012 survey and MINDEF areas carried over from 2007. The density of macaques for all areas that contained macaques was 0.46 social units per km^2 , and 6.86 ind km^{-2} . Core area density (i.e., zones one to four) was 0.97 social units km^{-2} , and 23.64 ind km^{-2} . Across all six survey regions, we found a range of 0.25–1.43 groups per km^2 , and 0.89–33.63 ind km^{-2} (Table 4). Of 1810 macaques, 1636 (90.4%) were found in the core area (Fig. 2). The mean group size was significantly larger for groups within the core area ($N = 60$, $M = 25.17 \pm 9.73$) than for groups outside it ($N = 9$, $M = 12.89 \pm 11.82$), (independent samples t-test: $t(67) = -3.433$, $P = 0.001$).

We calculated mean group sizes for each of the six survey regions. Mean group sizes ($\pm SD$) were as follows: MacRitchie region 23.86 ± 9.13 ; Bukit Timah region 28.41 ± 11.36 ; Old Upper Thompson region 24.58 ± 6.68 ; Mandai region 23.10 ± 11.07 ; Islands 16.56 ± 8.52 ; and Other region 11.46 ± 8.65 .

A Kruskal-Wallis test showed that group sizes were not equal across the six survey regions ($H(5) = 26.30$, $P < 0.001$). We conducted Dunn-Bonferroni post-hoc pairwise comparisons, which corrected for multiple comparisons. These tests showed that the Other region ($M = 11.46 \pm 8.65$) was significantly lower than the Bukit Timah region ($M = 28.41 \pm 11.36$), ($t = 39.15$, $P < 0.001$), MacRitchie region ($M = 23.86 \pm 9.13$), ($t = 29.86$, $P = 0.004$), and Old Upper Thompson region ($M = 24.58 \pm 6.68$), ($t = 33.39$, $P = 0.006$), but did not differ significantly from the Mandai region ($M = 23.10 \pm 11.07$), ($t = 27.57$, $P = .084$) or Island region ($M = 16.56 \pm 8.52$), ($t = 12.38$, $P = 1.000$). None of the other surveyed regions differed significantly from one another across group size.

Comparison with 2007 census. In 2007, the population count was 1218–1454 individuals in 71–112 social units (Sha et al., 2009b), and in 2012 our estimate was 1810–2166 individuals in 128 social units. The best estimate of the population in 2012 was 1909 and in 2007 the best estimate was 1454. This is a difference of 455 individuals, and our survey had a 24% higher count. Since the number of macaques per group was higher in 2012, overall density of individuals was also slightly higher in 2012 (6.86 ind km^{-2} in areas that contained macaques) than 2007 (5.22 ind km^{-2} in areas that contained macaques). The density of social units was very similar between 2012 (0.46 social units per km^2) and 2007 (0.40 social units per km^2).

We also compared infant and sex ratios. In 2012, there were fewer infants per adult female than in 2007. We found 0.36 infants per female, while in 2007 there were 0.44 infants per female. The overall mean ($\pm SD$) adult male to adult female sex ratio for 2012 was 0.55, while the mean sex ratio per group was 0.63 ± 0.40 , which is the same as the ratio of 0.63 ± 0.36 reported by Sha et al. (2009b).

Table 3. Reports of macaques that were unverified by researchers. We gathered reports from complaints to NParks from November 2011 to November 2012 from conversations with the public, and from media coverage. Groups are bolded. Regions are: M = MacRitchie; O = Old Upper Thompson; Md = Mandai; I = Islands, Ot = Other.

Location	Region	Reported # of macaques
Source: Report to NParks		
Ang Mo Kio Town Garden West	Ot	3
Bishan Park	O	1
Circuit Road	Ot	1
Clementi Woods Park	Ot	2
Duchess Ave	Ot	1
Greenleaf Lane	Ot	1
Heartland Mall	Ot	1
Holland Grove View	Ot	1
Jln Peminpin	M	1
Jln Pintau	M	1
Jurong West St 64	Ot	1
Lentor Road	O	1
Lorong Ah Soo	Ot	1
Lower Seletar Reservoir Park	Ot	1
Mayflower Crescent	O	4
Oxford Road	Ot	1
Pasir Ris	Ot	1
Paya Lebar Way	Ot	1
Pearl's Hill	Ot	3
Potong Pasir Ave 1	Ot	1
Segar Road	Ot	3
Sembawang	Ot	2
Singapore Botanic Garden	Ot	1
Spottiswoode Park	Ot	1
Tavistock Ave	Ot	1
Third Avenue	Ot	1
Watten Rise	Ot	3
West Coast Park	Ot	1
Whampoa Drive	Ot	1
Yio Chu Kang Gardens	O	1
Thomson Green	O	2
Toh Guan Road	Ot	1
Ulu Pandan Park Connector	Ot	1
Upper Wilkie Road	Ot	1
Source: Report to Researchers		
Bedok Reservoir Park	Ot	1
Chinese Garden	Ot	1
Mount Pleasant	M	10
Sentosa Ropes Course	I	20
Southern Ridges	Ot	5
Springleaf	Md	10
Sungei Buloh	Ot	1
Source: Media Report		
Dover	Ot	1
Khatib MRT	Ot	1
Singapore Flyer	Ot	1
12 groups		67
32 single animals		32
Total		99

Table 4. Density and count data in the six regions surveyed during the 2012 survey. Density calculations include MINDEF estimates carried over from the 2007 census, but do not include public reports from 2012.

Zone	Area (km ²)	# Social Units	Social Unit Density (per km ²)	Individuals	Individual Density (per km ²)
Bukit Timah Bukit Timah, Dairy Farm, Zhenghua, Bukit Batok	16.00	17	1.06	483	30.19
MacRitchie MacRitchie, Bukit Brown, Sime Road	20.90	22	1.00	511	24.45
Old Upper Thompson Old Upper Thompson Rd, Lower & Upper Peirce	9.07	13	1.32	305	33.63
Mandai Upper Seletar, Mandai Rd	19.17	11	0.52	241	12.57
Islands Sister's, Sentosa, Coney, Ubin, Tekong	40.12	10	0.25	169	4.21
Other Admiralty Park, Yishun Park, other areas not within the defined regions	173.02	55	0.30	200	0.89
Total	278.28	128	0.46	1909	6.86

DISCUSSION

As we will discuss below, the Singapore macaque population is comparable to wild long-tailed macaque populations in terms of density, group size, and age-sex distribution, despite the Singapore population having access to human food resources and being heavily affected by human influence. One major human impact is that Singapore has been culling macaques at least since the 1970s, when all of the macaques in Singapore's Botanic Gardens were culled following complaints (Sha et al., 2009a). Culling has continued off and on since that time and culling was ongoing by AVA while we conducted our census. Unfortunately, our requests to review culling records were not permitted. Consequently, we do not know the number and locations of macaques culled. We therefore cannot assess how culling may have impacted our results, and what role culling might play in influencing the Singaporean macaques' population parameters. In 2013, the year following our study, the media reported that approximately 570 macaques were culled by AVA's program (Khew, 2014). That is a removal of about a third of the population in one year, which is a significant source of mortality, and the largest annual cull ever reported to date in Singapore. Despite regular culling there have been no reported studies conducted in Singapore to investigate the impact culling has on the structure of the population. Without studying the culling records in detail, we can only draw limited conclusions on which factors impact the size and characteristics of Singapore's macaque population.

Our estimate of Singapore's macaque population is larger than all previous estimates of the population (e.g., Teo & Rajathurai, 1997; Agoramoorthy & Hsu, 2006; Sha et al., 2009b); however, prior to the 2007 survey, all censuses were incomplete. Moreover, even at this count, Singapore's macaques do not exhibit any evidence of overpopulation. Long-tailed macaque population densities have a wide range of variation in natural conditions, ranging from 0.6–7.7 groups km⁻², and averaging around 55 individuals km⁻² (Fooden, 1995). Densities of macaques in Singapore are well within that range, and even the highest density at Old Upper Thompson zone (33.63 ind km⁻²) is only at a moderate level. If we compare Singaporean macaques to other synanthropic macaques (i.e., those living with and benefiting from humans, primarily from human food sources), we find Singapore's density is much less, even though provisioned. Typical synanthropic macaque densities are regularly higher than 100 ind km⁻² (Fooden, 1995), and have been reported to be as high as 1600 ind km⁻² in one case in Bali (Wheatley, 1989). Singaporean long-tailed macaques are nowhere near such extreme densities, and thus the Singaporean macaque population density is distinctly not comparable to other synanthropic populations. Rather, they compare better to wild populations.

We also did not find any symptoms of overpopulation. Malaivijitnond & Hamada (2008) have pointed out that where macaques are overpopulated in Thailand, they have shifted from natural forests to becoming more concentrated in human environments, such as temples. During our study,

Singapore's population was concentrated primarily in the core reserves or other forested areas, and we did not find macaques living entirely in human environments. That being said, the reserves and forested areas are not pristine wilderness and include residences, recreation parks, and country clubs, and thus do have some degree of human disturbance. However, these areas are still mostly forested and macaques have not moved much from these areas. If the macaque population were overcrowded, we would have seen more growth outside of this core area. Whether due to culling or the natural state of the population, Singaporean macaques did not show population-level symptoms of being overpopulated during our census.

Our findings also showed group sizes more comparable to unprovisioned populations of long-tailed macaques, rather than provisioned populations. The mean group size in Singapore is comparable to average group sizes of long-tailed macaques elsewhere in SE Asia (van Schaik et al., 1983; van Schaik & van Noordwijk, 1985; Fooden, 1995). Our mean group size of 24.2 is within the mean group size range of 12–25 reported in Fooden (1995), and is comparable to average group sizes reported for long-tailed macaques in wild and non-urban habitats. For instance, Wheatley (1982) reported a mean group size of 30 for common long-tailed macaques in the swamp forests of Southern Kalimantan, Indonesia, and van Schaik & van Noordwijk (1985) reported a mean group size of 27 for common long-tailed macaques and Simeulue long-tailed macaques (*M. f. fusca*) in forests in Sumatra and Simeulue Island, Indonesia, respectively. In contrast, synanthropic macaques in other parts of SE Asia can attain group sizes over 100 individuals (Fooden, 1995; Gumert et al., 2011). Provisioned long-tailed macaque groups in Thailand, primarily living around temples, had an average group size of 77 (Aggimarangsee, 1992), which is more than three times the mean in our study. Group sizes in Mauritius, where long-tailed macaques are an invasive species and capitalise on farmlands, also exceeded 70 (Sussman et al., 2011). Once again we can see that the Singaporean long-tailed macaques resemble natural populations, more so than human-disturbed populations.

Other characteristics of the Singapore macaque population also indicated a normal population structure. Among numerous groups reviewed by Fooden (1995), the range of within-group adult sex ratios was 0.14–1.67 males per female. In our study, all groups except for two had sex ratios within that range. The two groups that were outside of this range were ST01 (ratio = 2.00), and PU02 (ratio = 2.50). Both groups were on offshore islands (i.e., Sentosa and Ubin islands, respectively), which could have affected male migration patterns due to insular isolation. The finding that the male to female sex ratio of island groups was nearly two times higher than that of non-island groups is consistent with this assertion. Also at the population level, the adult male to female ratio in the Singaporean long-tailed macaque population was 0.54, which is within the range of population-level adult male to female ratios (0.22–0.90) reported in a meta-analysis by Fooden. Thus, as with other population parameters, here we can see no clear deviations

from typical long-tailed macaque populations, other than the island dwelling groups in Singapore.

There were three groups that were exceptionally large in Singapore compared to other groups we observed. All three of these groups ($N = 43$ and $N = 47$ in BTNR; $N = 48$ in MacRitchie, in the CCNR) were all observed regularly feeding on human food, which is probably an important factor in their attaining these large sizes. Previous studies found a positive correlation between birth rates and food availability (Suzuki et al., 1998; van Noordwijk & van Schaik, 1999). However, it could also be that larger groups out-compete smaller groups for access to human food resources.

We could not always verify public reports of macaques and thus we have concerns of their validity, or our inability to find reported groups. The high frequency of single animals reported by the public ($N = 32$), as compared to low numbers counted by researchers ($N = 2$), could have been because a few single animals were seen repeatedly, perhaps being males migrating. It could also have been due to over-reporting by the public. Some public reports of groups were also difficult to verify. For instance, macaques were reported in the Southern Ridges, but we were unable to locate there. Park officials reported seeing them, however, they were possibly wary of humans because they were being culled at that time (Lee, B., pers. comm.) due to a biting incident (Feng, 2011). Additionally, the group was also very small, making it difficult to locate.

Our primary finding was that we counted a higher number of macaques in 2012 (range: 1810–2166) than was counted in 2007 (range: 1218–1454) (Sha et al., 2009b). It is easy to draw a conclusion that the Singaporean macaque population increased by several hundred in five years. However, this result requires some consideration. First, the two studies differed in their methods, making direct comparisons difficult. Consequently, it is not possible to fully rule out methodological differences as one source of variation in counting. One methodological difference is that we took photographs of all individuals to disambiguate groups and confirm counts. Using photographs resulted in revisions to counts obtained in the field, which improved and increased counts. Secondly, conditions were better. We had two permanent researchers on the project. We also had the advantage of having Sha et al.'s (2009b) study, as well as numerous other accumulated reports, which provided an easy guide on where to search for macaques. This likely increased our efficiency to document known macaques, and find more.

Aside from possible methodological inconsistencies, we also do not know the effects of culling on these counts. Culling is an important variable for understanding population changes in Singapore's macaques because culling occurs regularly and at significant levels. We must consider that the 2007 population was small, and around 600–650 macaques had been culled in the years up to that census. Sha et al. (2009b) found many groups of less than 10 individuals, which is much smaller than typical group sizes. He also observed numerous single animal sightings. This could have been

the result of undercounting, and thus methodological. Or, perhaps some groups were genuinely that small. Long-tailed macaques tend to have small group sizes where they have been hunted (Wheatley et al., 1999), and thus atypically small group sizes could have been a symptom of heavy culling. The count difference between 2007 and 2012 may have been a population rebounding from culling. Indeed, the difference in counts between 2007 and 2012 was around 450–700 individuals, which is comparable to the 600–650 macaques culled between 2002 and 2007. However, this comparison is limited by not knowing the levels of culling between 2008 and 2012. These figures do indicate though, that research on culling records is a necessary factor to include when assessing Singaporean macaque population trends.

To assess if the population was growing during our census, we can look for markers of population growth, such as age ratios in order to assess changes in birth rates. Singapore does not have immigration from other macaque populations, thus any population growth would be from reproduction. If the population was rapidly growing, we would expect a large amount of the population to be below five or six years of age; however, we found that the age ratio did not indicate an atypically high percentage of immature individuals. The ratio of young to mature was not higher in 2012 than 2007. Moreover, in our study, 56% of the population was immature, which is comparable to the composition of most natural long-tailed macaque populations (Fooden, 1995). Looking at infants, we found the infant to adult female ratio (1:2.81) in 2012 was lower than the ratio (1:2.3) in 2007 (Sha et al., 2009b), which does not support a faster reproductive rate in 2012 than in 2007. Better information is needed on rates of reproduction across years. Additionally, we must also consider what effects culling might have had, since young are disproportionately caught during culls.

In moving forward, we also need better assessment of the causal factors behind complaints. NParks initiated this study in response to a surge in macaque complaints. Without research on the reasons for increasing complaints, we cannot draw conclusions about the factors driving human-macaque conflict in Singapore. Since complaining drives culling, this is important. It is generally assumed that rising animal populations drive complaints regarding conflict; however, it is quite possible the reverse is true. Rather than an abnormal number of macaques, it may simply be that the increasing human population of Singapore (from 4.6 million in 2007 to 5.3 million in 2012; SingStat, 2012) is the primary driver of human-wildlife conflict. Indeed there has been extensive development of housing complexes, particularly near forested areas, in Singapore during the time periods assessed in our study, and during Sha et al. (2009b). Another potential influence on complaint increases was the opening of the AVA hotline in 2012 (Feng, 2013), which preceded the large 2013 cull.

Our census showed that Singapore has a macaque population exhibiting parameters within the range of wild non-provisioned populations of long-tailed macaques throughout SE Asia, and does not appear overpopulated or atypical like

some other synanthropic populations of macaques. Ideally, regular monitoring of this population should continue into the future in order to document demographic patterns across time. Furthermore, future monitoring of the population should attempt to standardise census methodology, to ensure more accurate analyses of population trends over time. Finally, it is necessary to note that monitoring is incomplete and limited in its usefulness unless culling records are also assessed. In-depth investigation into the effects of culling on the health and structure of the macaque population is critical for understanding population trends in Singaporean long-tailed macaques.

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LITERATURE CITED

- Afendi N, Rachmawan D & Gumert MD (2011) The long-tailed macaques of Karimunjawa (*Macaca fascicularis karimondjiwae*): A small and isolated island subspecies threatened by human-macaque conflict. In: Gumert MD, Fuentes A & Jones-Engel L (eds.) *Monkeys on the Edge: Ecology and Management of Long-tailed Macaques and Their Interface with Humans*. Cambridge University Press, Cambridge. Pp. 12–14.
- Aggimarangsee N (1992) Survey for semi-tame colonies of macaques in Thailand. *Natural History Bulletin of the Siam Society*, 40: 103–166.
- Agoramoorthy G & Hsu MJ (2006) Population status of long-tailed macaques (*Macaca fascicularis*) in Singapore. *Mammalia*, 70: 300–302.
- Altmann J (1974) Observational study of behavior: Sampling methods. *Behaviour*, 49: 227–265.
- Corlett R (1992) The ecological transformation of Singapore. *Journal of Biogeography*, 19: 411–420.
- Dice LR (1938) Some census methods for mammals. *Journal of Wildlife Management*, 2: 119–130.
- Feng Z (2011) Forest walk at HortPark: Attacks spark hunt for monkey. *The Straits Times*, October 7th. <http://www.straitstimes.com> (8 January 2013)
- Feng Z (2013) More reports on animal cases to AVA. *Straits Times*, March 11th. <http://www.straitstimes.com> (14 September 2015)
- Fooden J (1995). Systematic review of Southeast Asian longtail macaques, *Macaca fascicularis*, (Raffles, [1821]). *Fieldiana: Zoology New Series*, 81: i–206.
- Fuentes A, Kalchik S, Gettler L, Kwiatt A, Konecki M & Jones-Engel L (2008) Characterizing human-macaque interactions in Singapore. *American Journal of Primatology*, 70: 879–883.

- Gumert MD (2011) The common monkey of Southeast Asia: Long-tailed macaque populations, ethnophoresy, and their occurrence in human environments. In: Gumert MD, Fuentes A & Jones-Engel L (eds) *Monkeys on the Edge: Ecology and Management of Long-tailed Macaques and Their Interface with Humans*. Cambridge University Press, Cambridge. Pp. 3–44.
- Gumert MD, Fuentes A & Jones-Engel L (eds.) (2011) *Monkeys on the Edge: Ecology and Management of Long-tailed Macaques and Their Interface with Humans*. Cambridge University Press, Cambridge, 380 pp.
- Gumert MD, Hamada Y & Malaivijitnond S (2013) Human activity negatively affects stone tool-using Burmese long-tailed macaques *Macaca fascicularis aurea* in Laem Son National Park, Thailand. *Oryx*, 47: 535–543.
- Gumert MD, Rachmawan D, Iskandar E & Pamungkas J (2012) Populasi monyet ekor panjang (*Macaca fascicularis*) di Taman Nasional Tanjung Puting, Kalimantan Tengah. *Jurnal Primatologi Indonesia*, 9: 3–12.
- Gunasingham A (2011) Monkey nuisance: Complaints rose 30% last year. *Straits Times*, January 24th. <http://www.straitstimes.com> (14 September 2015)
- Khew C (2014) Monkey see, monkey do as the guard says? *Straits Times*, October 23rd. <http://www.straitstimes.com> (13 January 2015)
- Lucas PW (1995) Long-tailed macaques. *The Gardens' Bulletin Singapore*, Supplement 3: 105–119.
- Malaivijitnond S & Hamada Y (2008) Current situation and status of long-tailed macaques (*Macaca fascicularis*) in Thailand. *Natural History Journal of Chulalongkorn University*, 8: 185–204.
- Malaivijitnond S, Vazquez Y & Hamada Y (2011) Human impact on long-tailed macaques in Thailand. In: Gumert MD, Fuentes A & Jones-Engel L (eds) *Monkeys on the Edge: Ecology and Management of Long-tailed Macaques and Their Interface with Humans*. Cambridge University Press, Cambridge. Pp. 118–156.
- National Parks Board, Singapore (2009) Bukit Timah Nature Reserve. http://www.nparks.gov.sg/cms/index.php?option=com_visitors_guide&task=naturereserves&id=46&Itemid=75 (Accessed 10 October 2013)
- Riley CM, DuVall-Lash AS, Jayasri SL, Koenig BL, Klegarth AR & Gumert MD (in press) How living near humans affects Singapore's urban macaques. In: Waller M (ed) *Ethnoprimateology: Primate Conservation in the 21st Century*, Springer, New York.
- Ross C & Reeve N (2003). Survey and census methods: Population distribution and density. In: Setchell JM & Curtis DJ (eds) *Field and Laboratory Methods in Primatology: A Practical Guide*. Cambridge University Press, Cambridge. Pp. 90–109.
- Sha JCM, Gumert MD, Lee BPY-H, Jones-Engel L, Chan S & Fuentes A (2009a) Macaque-human interactions and the societal perceptions of macaques in Singapore. *American Journal of Primatology*, 71: 825–839.
- Sha JCM, Gumert MD, Lee BPY-H, Fuentes A, Rajathurai S, Chan S & Jones-Engel L (2009b) Status of the long-tailed macaque *Macaca fascicularis* in Singapore and implications for management. *Biodiversity and Conservation*, 18: 2909–2926.
- SingStat (2012) Key annual indicators. Singapore Department of Statistics, Government of Singapore, Singapore. <http://www.singstat.gov.sg/stats/keyind.html> (Accessed 30 October 2012)
- Sussman RW, Shaffer CA, Guidi L (2011) *Macaca fascicularis* in Mauritius: Implications for macaque-human interactions and for future research on long-tailed macaques. In: Gumert MD, Fuentes A & Jones-Engel L (eds) *Monkeys on the Edge: Ecology and Management of Long-tailed Macaques and Their Interface with Humans*. Cambridge University Press, Cambridge. Pp 207–235.
- Suzuki S, Noma N & Izawa K (1998) Inter-annual variation or reproductive parameters and fruit availability in two populations of Japanese macaques. *Primates*, 39: 313–324.
- Teo RCH & Rajathurai S (1997) Mammals, reptiles and amphibians in the nature reserves of Singapore – Diversity, abundance and distribution. *The Gardens' Bulletin Singapore*, 49: 353–425.
- van Noordwijk MA & van Schaik CP (1999) The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed macaques, *Macaca fascicularis*. *Primates*, 40: 105–130.
- van Schaik CP & van Noordwijk MA (1985) Evolutionary effect of the absence of felids on the social organization of the macaques on the island of Simeulue (*Macaca fascicularis fusca*), Miller 1903). *Folia Primatologica*, 44: 138–147.
- van Schaik CP, van Noordwijk MA, de Boer RJ & den Tonkelaar I (1983) The effect of group size on time budgets and social behaviour in wild long-tailed macaques (*Macaca fascicularis*). *Behavioral Ecology and Sociobiology*, 13: 173–181.
- Wheatley BP (1982) Energetics of foraging in *Macaca fascicularis* and *Pongo pygmaeus* and a selective advantage of large body size in the orang-utan. *Primates*, 23: 348–363.
- Wheatley BP (1989) Diet of Balinese temple monkeys, *Macaca fascicularis*. *Kyoto University Overseas Research Report of Studies on Asian Non-Human Primates*, 7: 62–75.
- Wheatley B, Stephenson R & Kurashina H (1999) The effects of hunting on the longtailed macaques of Ngeaur Island, Palau. In: Dolhinow P & Fuentes A (eds.) *The Nonhuman Primates*. Mayfield Publishing Company, Mountain View, CA. Pp. 159–163.