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Thesis

Ecology of Long-Tailed Macaques (*Macaca fascicularis*) and its Implication for the Management of Human-Macaque Interface in Singapore

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Chapter I

General Introduction

1. The human-nonhuman primate interface

Human and nonhuman primates are close evolutionary relatives that are culturally, economically and ecologically interconnected throughout many parts of the world (Fuentes & Wolfe, 2002; Fuentes & Hockings, 2010; Loudon et al., 2006; Riley et al., 2011; Sponsel et al., 2002; Wheatley et al., 2002). Primates are highly symbolic across many Asian cultures. In Japan, the Japanese macaque (*Macaca fuscata*) is central to many aspects of Japanese cosmology during different historical periods (Asquith, 1986; Ohnuki-Tierney, 1991). The monkey is similarly entrenched in Chinese mythology, as the "Monkey King" in one of the four great classical novels of Chinese literature "Journey to the West" (Wu, 1961). In Buddhism, the monkey is regarded as an early incarnation of the Buddha and similarly, in Hinduism, the human-like monkey god "Hanuman" is regarded as a prominent divine entity in the "Ramayana" (Burton, 2002; Fuentes, 2007). In Thailand, macaques are associated with religious systems and are often integrated into festivals and celebrations (Malaivijitnond et al., 2011).

The cultural connections between human and nonhuman primates have contextualized interactions between the two. Levels of tolerance, acceptance and even demand for interactions with primates vary with cultural context (Biquand et al.,

1992; Burton, 2002; Gautier & Biquand, 1994). Positive cultural connections have directly or indirectly led to the prevalence of primate food provisioning and associated "monkey temples" across many Asian countries where primates are considered sacred or inhabit landscapes that are considered as such (Aggimaransee, 2002; Eudey, 1994; Fuentes et al., 2005; Loudon et al., 2006; Sponsel at al., 2002). At sites associated with Buddhism or Hinduism in China, India and Indonesia, temple practitioners and pilgrims regard interacting and feeding primates as a way to acquire spiritual merit (Fuentes et al., 2005; Medhi et al., 2007; Zhao, 2005). In many places with human-primate conflicts, for example, in India and Sulawesi, cultural tolerance alone is protecting primate species (Lee & Priston, 2005; Riley & Priston, 2010). In Japan, cultural connections between human and nonhuman primates have been invoked against the background of rising human-macaque conflict, in the form of natural and nationalistic symbolism and *kyosei* or coexistence as a conflict management philosophy (Knight, 1999; Sprague & Iwasaki, 2006; Watanabe, 1996).

The economic interface between human and nonhuman primates occurs in different contexts. An exploitative relationship occurs through hunting for bush meat, pet trade, trophies, entertainment industry, traditional medicine and the biomedical industry (Alves et al., 2010; Fa et al., 2006; Kavanagh, 1984; Nijman et al., 2011; Southwick & Siddiqi, 2001). Many primates, particularly those of the genus *Macaca*, are widely used in the biomedical and technological sciences industries (Foley & Shepherd, 2011; Hagelin, 2004). Cooperative relationships exist, for example, in Thailand, where pig-tailed macaques (*Macaca nemestrina*) are trained to pick coconuts, yielding high economic returns (Sponsel et al., 2002). Economic

relationships also occur increasingly through primate tourism (Fuentes et al., 2007; Kinnaird & O'Brien, 1996; Knight, 2011). Monkey tourism at temple sites in Bali, Lombok and Thailand provide significant sources of revenue for local communities (Fuentes, 2006b; Hadi, 2005; Malavijitnond & Hamada, 2008; Malavijitnond et al. 2011; Wheatley & Putra, 1994). Interface also occurs within forest reserves and national parks where primates are habituated and interact with tourists, for example in Tangkoko, Sulawesi (Kinnaird & O'Brien, 1996) and Pangandaran, West Java (Engelhardt, 1997). In the case of primate tourism, the relationship between humans and primates may not be entirely mutualistic due to conflict issues arising from primate aggression and resultant conflict issues (Gumert, 2011). Human and nonhuman primates also interact within agricultural landscapes, with crop-raiding by primate species contributing to major economic consequences for farming communities throughout Asia (Campbell-Smith et al., 2010; Lee & Priston, 2005; Pirta et al., 1997; Umapathy et al., 2003; Wheatley et al., 1996).

The ecological interface between human and nonhuman primates occurs through recent and long-term sympatries, and is central to the behavioral ecology, conservation, and evolutionary trajectories of countless primates (Paterson & Wallis, 2005; Riley, 2007; Wolfe & Fuentes, 2006). Such ecological interface is due mainly to human modifications of natural landscapes and associated crop-raiding and related resource exploitation patterns by primate species (Fuentes & Hockings, 2010; Loudon et al., 2006). For example, in Bali, agricultural and land-use patterns, combined with complex temple and irrigation systems has resulted in habitats that fit remarkably well with patterns of habitat use, foraging and dispersal of long-tailed macaques (*Macaca fascicularis*), leading to increased interface with humans

(Fuentes et al., 2005; Fuentes & Hockings, 2010; Lane et al., 2010). Populations of primates living close to humans are becoming more prevalent due to natural habitat shrinkage, increasing the potential for interface with humans, and often resulting in conflict situations (Fuentes & Wolfe, 2002). Close interface can significantly increase the risks of cross-species transmissions of diseases like herpes B and simian foamy virus, amongst others (reviewed in Engel & Jones-Engel, 2011). There is increasing recognition of the continued increase in spatial and ecological overlap between human and nonhuman primates; the importance of understanding contributing factors to primate behavioral adaptations in anthropogenic influenced habitats; and the consequences for both human and primate populations interfacing with one another (Fuentes & Hockings, 2010; Fuentes, 2012).

2. Anthropogenic influence on primate behavior and ecology

Many primate populations now inhabit anthropogenic-influenced landscapes where they have access to human food (Fuentes & Wolfe, 2002; Saj et al., 1999; Strum, 2010; Treves, 2009). Anthropogenic food is often palatable, energy-rich, easily digestible, spatially clumped and abundant; offering energetic advantages over natural food (Forthman-Quick, 1986; Forthman-Quick & Demment, 1988; Saj et al., 1999). Generalist species with high dietary plasticity adjust more readily to altered conditions in anthropogenic-influenced habitats (Onderdonk & Chapman, 2000; Vasquez & Simberloff, 2002). For some of these species, anthropogenic food sources, such as cultivated plants or refuse, can become an integral part of their diet (e.g. Fuentes et al., 2011; Lee et al., 1986; Richard et al., 1989; Schurr et al., 2012; Strum,

1994). In provisioned Barbary macaques, for example, anthropogenic food resources make up as much as 76% of their total diet (Schurr et al., 2012).

The inclusion of high-quality foods from anthropogenic sources can significantly influence primate behavioral characteristics (e.g. Fuentes et al., 2005; 2011; Hadi et al., 2007). These effects are often reflected by smaller home ranges and shorter day ranges, less time travelling and feeding and more time resting (e.g. Altmann & Muruthi, 1988; Forthman Quick & Demment, 1988; Malik & Southwick, 1988; Kogenezawa & Imaki, 1999; Saj, 1999; Strum, 2010; Wheatley et al., 1996). The effects of anthropogenic food utilization can minimize seasonal differences in behavior and physiology that is otherwise determined by natural resource factors, further complicating their relationship (Altmann & Muruthi, 1988; Van Doorn et al., 2010). Management of human-commensal mammals that show a high degree of behavioral flexibility in response to habitat and resource variability is playing a growing role in their continued survival, increasing the importance for understanding how a combination of different anthropogenic and ecological pressures may together influence their behavioral ecology (Jaman & Huffman, 2013; Treves et al., 2006; Tsuji, 2010; Van Doorn et al., 2010).

3. The long-tailed macaque

The long-tailed or crab-eating macaque occupies a broad geographical range extending across the greater part of mainland Southeast Asia (Fooden, 1995; 2006). The species is considered one of the most abundant non-human primate species within its native range (Wheatley, 1999). It is classified by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species as "Least

Concern", and under Appendix II of the International Convention for the International Trade of Endangered Species (CITES). The wide range, abundance and limited protection of long-tailed macaques throughout their range gives the impression that the species is unthreatened, with management authorities in areas with human-macaque conflict often regarding them as expendable pest species with little ecological or conservation value. Populations of long-tailed macaques are however, believed to be rapidly declining in many areas due to habitat loss, degradation, conflict with humans, and trapping for commercial trade (Eudey, 2008; Lee, 2011).

Long-tailed macaques are found naturally in a wide variety of habitats including primary, secondary, coastal, mangrove, swamp, and riverine forest (Crockett & Wilson, 1980; Wolfheim, 1983). They adapt well to altered and stochastic environments (Poirier & Smith, 1974; Wheatley, 1999), and often exploit environments affected by human settlement and agriculture (Bismark, 1991; Fuentes et al., 2005; Richard et al., 1989). They exhibit riverine refuging behavior and are most commonly found along forest edges, especially in swamp and riverine forests (Bismark, 1991; Crockett & Wilson, 1980; Fittinghoff & Lindburg, 1980; van Schaik et al., 1996; Wheatley, 1980). In riparian forests, they occur mostly within 100 m of rivers (Crockett & Wilson, 1980; Bismark 1991) and at higher densities compared to interior forests (McConkey & Chivers, 2004). These characteristics of long-tailed macaque habitat preference and adaptability increase the likelihood of close proximity with humans. Due to anthropogenic land-use increasingly generating large amounts of forest edges, they are commonly reported to inhabit the edges of a variety

of anthropogenic habitats (Fuentes, 2006b; Hadi, 2005; Malaivijitnond & Hamada, 2008; Wong & Ni, 2000).

Long-tailed macaques have relatively long lifespans averaging 25 years and also exhibit high fecundity (Ross, 1991). When habitat and food resource conditions are favorable, long-tailed macaques can achieve very high birth rates - 53% per year in natural populations (van Noordwijk & van Schaik, 1999) and up to 72.5% per year in populations with access to anthropogenic foods (Aggimarangsee, 1992; Fellowes, 1992; Southwick and Southwick; 1983; Wong & Ni, 2000). Such high fecundity and resultant population growth has often been linked to increased human-macaque conflict. They generally achieve larger group sizes in disturbed habitats compared to pristine forests (O'Brien & Kinnard, 1999; Sussman & Tattersall, 1986) which is attributed to greater abundance of food in these habitats, as well as a possible access to agricultural crops along the forest edge. Long-tailed macaques with access to human provisioning can achieve even larger group sizes, reported to reach up to 200 individuals in Thailand (Malaivijitnond & Hamada, 2008). Density estimates for the long-tailed macaque range from 4 to 121 individuals/km^2 in naturalistic or semi-naturalistic habitat conditions (Crockett & Wilson, 1980; Supriatna et al., 1996; Wheatley, 1999). Densities in primary forests are generally lower compared to swamp and mangrove forests and secondary forests, disturbed and cultivated habitats. In urban habitats, densities can reach 326 to 1111 individuals/km^2 (Wheatley, 1996; Wong & Ni, 2000). High densities of long-tailed macaques, when interfaced with human populations can be a contributing factor to actual or perceived conflict problems between the two.

Long-tailed macaques are omnivorous but predominantly frugivorous, with a major composition of natural diet made up of fruits, but they also feed on flowers, buds, leaves, bark, roots, pith and animal prey (Aldrich-Blake, 1980; Lucas & Corlett, 1991; Yeager, 1996). In human-commensal long-tailed macaque populations, anthropogenic foods may make up 20% to 99% of their diet, with consequence reduction in natural diet (Aggimarangsee, 1992; Fa, 1986; Fuentes et al., 2005; 2011). Such dietary flexibility allows long-tailed macaques to significantly alter their foraging strategies to exploit resources found in anthropogenic-influenced habitats. Activity and ranging patterns associated with anthropogenic resource exploitation can lead to increased interface between humans and macaques, leading to conflict situations.

4. Singapore and the long-tailed macaque situation

Singapore (103°500E, 1°200N) is located off the southern tip of Peninsular Malaysia and covers an area of approximately 714.3 km^2 (MTI, 2012). Before 1819, Singapore was covered with dense rainforest, but in the last two centuries, land conversion for agriculture and recent urbanization has resulted in more than 95% of the original forest being converted to residential, industrial and recreational use with current forest cover represented by natural and semi-natural forest fragments scattered in highly urbanized environments (Corlett, 1992; Turner et al., 1994). Most of the remaining forest is concentrated within the Central Catchment Nature Reserve (CCNR) (2,000 ha) and Bukit Timah Nature Reserve (BTNR) (164 ha). These reserves are adjacent to periphery forested and non-forested areas like military

restricted training grounds, golf courses and recreational park areas, and bounded entirely by roads and expressways.

Considerable ecological transformation in the last two centuries has resulted in significant losses to Singapore's original biota (Brook et al., 2003; Castelletta et al., 2000; Corlett, 1992). Vertebrate populations have declined and all large terrestrial mammals are now locally extinct (Corlett, 1992). In spite of these dramatic changes to Singapore's natural forest, long-tailed macaques have persisted and are one of the last remaining medium-sized mammals with a sizable know population and wide distribution in Singapore. It is also one of three remaining primate species found in Singapore, the others being the banded langur (*Presbytis femoralis femoralis*) and the slow loris (*Nycticebus coucang*). In Singapore, long-tailed macaques are protected by law under the Wild Animals and Birds Act (Chapter 351).   The current population of long-tailed macaque is highly conspicuous and they frequently interface with humans in settlements and recreational areas around Singapore's nature reserves and parks. The close interface between macaques and humans has led to conflict, with the first problematic situation recorded in Singapore at the Botanic Gardens during the 1960s (Harrisson, 1966; Medway, 1969). Eventually, this conflict led to the eradication of those macaques in the 1970s (Tan et al., 2007). Reports of human-macaque conflict have since continued in other parts of Singapore (Corlett, 1996; Lucas, 1995). In recent years, there are numerous popular reports of this conflict situation (Murdoch, 2007; Mulchand & Tan, 2008). Public complaints about nuisance macaques have increased since the turn of the century, with the mean number of public complaints between 2001 and 2007 more than double that between 1996 and 2000 (Agri-Food and Veterinary Authority, in litt.). The complaints

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received have mainly come from people living in residential areas along the periphery of the BTNR and CCNR. Unlike many other countries experiencing problems with macaque crop-raiding, for example, in Papua New Guinea where introduced macaques raid crops amounting to losses of approximately USD $3,500 per year (Kemp & Burnett, 2003); Singapore does not have any agricultural industry of note. The problems commonly associated with macaque damage related more to damage to privately planted fruit trees, theft of food, etc. The rise in complaints about conflicts with macaques may thus indicate an increase in direct interactions between humans and macaques.

5. Outline and summary of this study

The main aim of this study is to examine various aspects of the ecology of long-tailed macaques in Singapore to identify important contributing factors to increasing human-macaque interface and resultant conflicts. Findings are considered in the context of human-macaque conflict mitigation to guide more holistic and scientifically informed management measures.

My investigation begins in Chapter II - "Status of the long-tailed macaque *Macaca fascicularis* in Singapore and implications for management". The objective of this chapter is to provide a macro view of the situation of long-tailed macaques in Singapore by assessing population, distribution and life history parameters in the context of habituation and provisioning. A key finding from this chapter was that absolute increase in population size over the past two decades was not large but macaque populations were mostly distributed in forest edge habitats adjacent to human habitation and activities, resulting in the close association between humans

and macaques. A significant proportion of macaques were also habituated and/or provisioned, and these groups attained larger group sizes and higher infant: adult female ratios. The results from this chapter set the stage for more detailed considerations into various aspects of long-tailed macaque behavior and ecology in anthropogenic-influenced habitats.

In Chapter III – "Macaque-human interactions and the societal perceptions of macaques in Singapore", the objective is to contextualize macaque behavior towards humans, the contributing factors for such interactions, and human perceptions towards macaques and their management. A key finding from this chapter was that overall interactions between macaques and humans were relatively low and the human-macaque conflict situation in Singapore could be considered one of the most benign in the world, compared to other countries with human-primate interface. There was also ample public support for maintaining a macaque population, despite conflict issues, setting the tone for management authorities to consider a more holistic management approach.

In Chapter IV – "Diet, activity, habitat use, and ranging of two neighboring groups of food-enhanced long-tailed macaques (*Macaca fascicularis*)", the objective is to investigate the behavioral and ecological aspects of Singapore long-tailed macaques in the context of food-enhancement. This chapter revealed information on the diet, activity, habitat use, and ranging of two groups of long-tailed macaques that inhabit both natural forest and urban habitats; and the comparative effects of food-enhancement. A key finding from this chapter was that within-group variations in behavior and ecology existed in overlapping groups at the same site and the effects of food-enhancement contrasted with what was typically shown in other studies. This

was due to the nature of anthropogenic foods being spatially dispersed and limited, compared to other studies where these foods were abundant and concentrated. These results have important implications for mitigating human-macaque conflict as measures applied at a higher spatial or population level may achieve highly inconsistent results.

In Chapter V – "Temporal food resource correlates to the behavior and ecology of food-enhanced long-tailed macaques (*Macaca fascicularis*)", the objective is to examine how macaque behavior and ecology correlate to temporal natural and anthropogenic resource availability. A key finding from this chapter was that dietary compositions of the macaques were correlated to natural fruit availability; but activity, habitat use and ranging patterns were correlated more to food availability from refuse sites and provisioning. Higher feeding on anthropogenic food resources did not occur in times of higher natural food scarcity. These results showed that the main drivers for macaque exploitation of anthropogenic foods were unlikely to be either natural food resource scarcity or a high dependence on anthropogenic foods.

Chapter VI synthesizes the findings from the preceding chapters by identifying the key contributing factors for human-macaque interface and conflict and discusses how these factors have implications for the long-term management of long-tailed macaques in Singapore. Comparisons are also made to the human-macaque conflict situation in Japan. Recommendations for human-macaque conflict mitigation are provided to assist in the consideration for more effective approaches to management. A section on limitations of this study and suggestions for further studies is also included at the end of this chapter.

Chapter II

Status of the long-tailed macaque (*Macaca fascicularis*) in Singapore and implications for management

1. Abstract

The long-tailed macaque (*Macaca fascicularis*) population of the island-state of Singapore consists of ca. 1,228–1,454 individuals. About seventy percent of the population (ca. 1,027 individuals) is concentrated in both Bukit Timah and Central Catchment Nature Reserves, a system of reservoirs and forest reserves located in the center of Singapore. This core population resides mainly along perimeter forest areas of the reserve system, which is bordered by residential and recreational areas (e.g., parks and golf courses) and encircled by expressways. Periphery sub-populations (ca. 427 individuals) persist in forest fragments throughout Singapore mainland and on 5 offshore islands. Much of the Singaporean macaque population overlaps with human settlement and these commensal groups are mainly distributed close to roads, parks and residential areas. At least 70% of these groups are habituated to human presence and at least 50% to food provisioning. Moreover, commensal groups have more individuals and have higher infant:adult female ratios than non-commensal groups. The close association of habituated macaque groups living in human environments has led to increasing human-macaque conflict in Singapore. The overlap is also

associated with human-induced population loss resulting from road accidents (2.4%); and trapping efforts (14%) aimed at ameliorating conflict issues. Consequently, it is important to better understand how humans are affecting macaque populations. In order to mitigate human-macaque conflict and at the same maintain a sustainable macaque population in Singapore, there is an urgent need for wildlife management strategies aimed at minimizing the extent of human-macaque conflict. Such strategies should include designing appropriate buffers around reserve areas, revised urban development plans, and managing the behavior of people interfacing with macaques.

2. Introduction

In many regions where human-macaque conflict occurs, the problem is often assumed to be the result of large macaque populations being sympatric with human populations. This perspective frequently drives management decisions to cull, translocate, or export in an effort to lower macaque population sizes to ameliorate the source of the conflict (e.g. Malaysia: Associated Press, 2007 and India: NDTV, 2007). Curiously, little focused investigation on long-tailed macaque populations in areas of high human density has been conducted and thus it remains premature to conclude that it is simply the large macaque population in contact with human populations that is the main contributor to significant conflict. Other factors, such as human encroachment and behavior towards monkeys (e.g., feeding) also can largely influence conflict with macaques, independent of population size, and therefore human influences may be the initial trigger of conflict, rather than macaque population growth.

It is important to begin assessing long-tailed macaque populations that conflict with humans in order to uncover the root cause of these conflicts. In Singapore, previous censuses have been conducted on the macaque population. In a survey conducted in 1986, the Malayan Nature Society estimated that the macaque population does not exceed 1,000 on Singapore island (Lucas, 1995). In more recent surveys, ca. 635 to 850 individuals were estimated within the nature reserves (Agoramoorthy & Hsu 2006; Teo & Rajathurai, 1997). These censuses have not been followed up and therefore it is unclear whether the macaque population in Singapore has significantly increased since these population counts. Consequently, it is unclear whether population growth is the main primer for the increasing reports of human-macaque conflicts that have occurred in Singapore over the last several years. In order to answer this question and determine the current status of Singapore's macaques, we conducted a census on the population size for Singapore in the nature reserves, parks, other forest fragments, and smaller offshore islands. During this survey I determined the macaques' distribution and population dynamics (i.e., sex ratio, birth and growth indexes) and related these measures to levels of habituation, provisioning and association with humans. This research provides important information for the long-term monitoring and management of the long-tailed macaques of Singapore, as well as providing information on the factors influencing human-macaque conflict.

3. Methods

3-1 Distribution, population size and density

Surveys were conducted from April to November 2007 within the Bukit Timah Nature Reserve and Central Catchment Nature Reserve (herein collectively referred to as NR), the Western Catchment and forest fragments throughout the island (Figure 1a). Within the NR, macaques were surveyed using census walks (Dowhinow & Lindburg, 1980; Wilson et al., 1996) in the mornings (0700 to 0900 h) and evenings (1600 to 1900 h) to locate and count groups of macaques along existing trails and roads. The census walks were conducted over 63 days and covered a total of 72.1 km of different trail systems within NR (Figure 2). The first author (JS) and one assistant walked along existing trails or roads to locate macaques through direct sightings, movements or vocalizations. Once a macaque sighting was confirmed, the surveyors stopped and collected the following data: (1) observed group size; (2) age-sex class of each individual; and (3) location plotted on a GPS (Trimble^{TM} Recon and GPS Pathfinder XB, Trimble Navigation Limited, USA). The surveyors then approached the group slowly to record (1) how the group responded to human presence; and (2) how the group responded to food cues. To verify the macaque groups observed from census walks, I identified individuals from the groups whenever possible from facial hair patterns, scars on bodies and tail kinks. "Sweep" surveys were also conducted, which involved different groups of observers surveying all the trails at the same time. These surveys helped identify the maximum number of groups along survey routes, as well as the sleeping sites for individual groups. In some groups, I was not able to confidently estimate group sizes during census walks and I therefore conducted follows of groups from their sleeping sites in order to repeat and gain more accurate counts. These follows lasted from 1 to 12 h, depending on the time needed to make an accurate count of the entire group.

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Surveys outside the NR and Western Catchment were chosen based on information gathered from existing published literature, newspaper articles and interviews with park and wildlife officials about macaque sighting locations. The sources of information included staff of the National Parks Board (NParks), Public Utilities Board (PUB), residents living near macaques, members of the public, other researchers and media sources (Table 1a, b). I conducted verification surveys to locate groups reported by these sources. Groups were considered reliable if reports were corroborated by more than one source or by a park or wildlife official source. If the verification survey on these reliable reports did not yield sightings for us, I used data on last sighted date and reported group size from our reliable source. Surveys were also conducted in some larger forested fragments where macaques have not been reported but were suspected to exist.

3-2 Population size and density

I estimated the population of macaques in Singapore. The population size for the NR was estimated by counting all groups and individuals observed during surveys. In addition to this count, I also added in counts for three relocated groups to an area within the CCNR and three groups living on the premises of Singapore Zoo and Night Safari area. The CCNR group was relocated to a remote part of the CCNR in 2005 and individuals in the group were individually identifiable by a zoo staff (B. Martelli) who monitored them up to 2007. The Singapore Zoo and Night Safari surveys were conducted by staff using "sweep" surveys.

The total population size for mainland Singapore was estimated from total group and individual counts of identified groups from surveys (lower limit) and in

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addition to reported numbers from various sources (upper limit). The population from offshore islands was taken purely from secondary sources and I did not conduct surveys on these islands for this study.

A rough density measure was calculated by dividing group and individual counts by the total area of NR and its periphery. This area included all adjacent forested and not-forest areas, such as military restricted areas, golf courses and recreational park areas bounded by the expressways, macaques were sighted to use, and excluding the water catchments (Figure 1b). Another density estimate was calculated for just the area covered by NR alone.

3-3 Age-sex class, sex ratio and reproductive index

During my survey counts of individuals, I also recorded age and sex. The age classes recorded were adult, adolescent, juvenile and infant. Discriminations of age and sex were done by visual assessment of body size, the genitalia, and the level of development of sexual organs and mammary development in females (Dittus & Thorington, 1981). Sex ratio was estimated by dividing the average number of males counted in a group by the average number of females from multiple group counts (Thompson, 1992). This method was used to reduce possible errors from one single absolute count. Sex ratio was only calculated for bisexual groups. An infant:adult female ratio was calculated by dividing the average number of infants counted in a group by the average number of adult females counted from multiple group counts. The infant: adult female ratio was used as an indicator of birth rate, since I could not measure birth rate directly.

3-4 Group habituation and provisioning

I categorized each macaque group by its level of habituation and amount of provisioning received. Each macaque group's level of habituation was classified into three categories; habituated, semi-habituated, and non-habituated. A group was categorized as habituated if it appeared accustomed to my presence and I could approach to within 10 m. A group was classified as semi-habituated if it was not approachable but could be observed from a distance of less than 10 m. A group was categorized as non-habituated if it actively avoided close contact and moved away from the researcher(s). Macaque groups were also classified according to whether they were provisioned or not. Provisioned groups were those that were observed directly to receive food from humans, forage on artificial human food sources, or respond to the researcher(s)' presented food cue using plastic bags. Non-provisioned groups were those that were not observed to receive food from humans, were not observed or reported to forage in human habitats, and did not show any obvious interest to human food-source cues. As crop-raiding by macaques is not relevant in the Singapore context, anthropogenic food exploitation usually occurs in the presence of humans. These methods thus sufficiently provided an estimation of habituation and anthropogenic food provisioning.

3-5 Mapping and GIS analysis

I used Global Positioning System (GPS) and Geographic Information System (GIS) to map the location of each group surveyed or reported macaque sleeping sites were marked by GPS (Trimble^{TM} Recon and GPS Pathfinder XB, Trimble Navigation Limited, USA) and used to plot the distribution of macaques. When

sleeping sites were unknown, the sighting location was plotted on the map instead. A gradient of distances of roads and human settlement from the center of the NR was generated using ''Buffer Wizard'' in GIS (ESRI ArcGIS[TM] 8.3, Environmental Systems Research Institute, USA 2005). This gradient measure produced bands of 100 m width between 0 and 1,700 m. I then overlayed the distribution of macaques onto these bands using GIS and counted the number of macaque groups that fell within each band. Lastly, I generated density patterns of the macaque population in NR from the mapped data using ''Spatial Analyst-Density'' in ArcGIS[TM].

3-6 Data analysis

I used correlation and regression techniques to determine relationships with numbers of macaques. I used Pearson correlation and Cubic regression to analyze the relationship between the number of macaque groups and the distance they were found from roads and human habitation. I used the same procedure to measure the relationship between the mean group size of macaque groups and distance for roads and settlement. Cubic regression was used to assess if the relationship was non-linear. I used linear regression to analyze the relationship between group size and infant: adult female ratio, to determine if group size could predict the reproductive output of a group. Spearman correlation was also used to test for the relationship between group size and sex ratio.

Correlation techniques were also used to determine relationships with complaints received. I used a Pearson correlation to test the relationship between the number of complaints received and number of macaques trapped. Spearman

correlation was used to analyze the relationship between the number of complaints with time and number of macaques trapped with time.

A Kruskal–Wallis test and a post-hoc Mann–Whitney U-test were used to test for whether habituated, semi-habituated and non-habituated groups differed in group size. Mann–Whitney U-tests were used to test for three other factors if a significant result was found in the Kruskal–Wallis test. First, I tested for differences in group sizes between provisioned groups and non-provisioned groups. Second, I tested for differences in infant:adult ratio for populations within the NR and isolated populations outside the NR. Thirdly, I tested whether the sex ratio varied between groups within the NR and those in forest fragments.

All data were checked for normality using Kolmogorov-Smirnov tests, and where data was not normal non-parametric statistical tests were chosen. All analyses were done using the Statistical Package for the Social Sciences version 16.0 (SPSS Inc., Chicago, IL). Statistical significance was set at $P < 0.05$.

4. Results

4-1 Population size, distribution and density

The survey count for the population was 1,027 individuals (including 2 solitary male counts) in the NR. Outside NR in forest patches scattered throughout the main island and on offshore islands, there were another 201 (including 1 solitary male count) to 426 individuals (including 9 solitary male counts) (Figure 1; Table 1a, b). Based on my counts and reports, I estimate that the total population for Singapore was 1,228 to 1,454 individuals. About 70% of the population was found within the main forested area of the NR and its periphery. I calculated the density of macaques

in the NR and its periphery to be 1.5 groups and 28.2 indiv./km^2. If I only consider

density based on area of NR, density was 2.5 groups and 47.6 indiv./km^2. The

density of macaques showed high concentrations within 3 specific reserve areas in

the NR. These were Bukit Timah, Upper Seletar and the regions of Upper Peirce to

Lower Peirce along Old Upper Thomson road (Figure 1c). It was also evident that

the number of macaque groups increased significantly with increasing proximity to

roads and human settlement - Pearson correlation: r = -0.666, $P = 0.036$ ($r^2 = 0.789$,

$P < 0.001$, F = 16.245, df1 = 3, df2 = 13) (Figure 3).

4-2 Group characteristics

The population's age structure was 47% adults, 20.2% adolescents, 20.1%

juveniles and 12.7% infants. The majority of verified groups were

multimale-multifemale (n=88). Mean group size of multimale-multifemale groups

was 13.7 ± SD 11.7 (range 3 to 66). 42.7% of observed groups were habituated,

30.8% semi-habituated and 26.5% non-habituated. 54.6% of groups were

provisioned and 45.4% non-provisioned.

Several factors influenced group size and sex ratio. Mean group size increased

with increasing proximity to roads and human settlement ($r^2 = 0.870$, $P = 0.005$, F =

13.440, df1 = 3, df2 = 6) (Figure 4). In addition, the level of habituation also

influenced group size (Kruskal–Wallis, $\chi^2 = 19.26$, df = 2, $P < 0.001$). Post-hoc

Mann–Whitney U-tests indicated that the mean group size of habituated groups was

25.2 ± SD 13.2 individuals and semi-habituated was 14.2 ± SD 5.9 individuals and

these were significantly larger than non-habituated groups averaging 10.9 ± SD 5.6

individuals. Provisioning was related to group size because provisioned groups (21.1

± SD 10.8) were larger than non-provisioned groups (12.1 ± SD 7.1) (Mann–Whitney U-test, U = 112.5, P = 0.001). Sex ratio of adult long-tailed macaques was found to be 0.63 ± SD 0.36, which is a male: female ratio of 1:1.6. The male: female sex ratio of groups in the main forested area of the NR and periphery (0.61 ± SD 0.34) was significantly lower than in forest fragments (0.89 ± SD 0.39) (Mann–Whitney U-test, U = 120.0, P = 0.012). Group size and sex ratio did not show a correlation (r_s = 0.168, P = 0.225, N = 54).

4-3 Birth and mortality

The number of infants and human-caused mortality were measured during this study. A maximum of 186 infants were observed during the study. An infant: adult female ratio of 1:2.3 in 2007 was derived from the average number of infants and females. The infant: adult female ratio was higher for groups within the reserves (0.45 ± SD 0.19) compared to isolated groups outside of the reserves (0.23 ± SD 0.22) (Mann–Whitney U test, U = 118, P = 0.011). The infant: adult female ratio was also higher for provisioned groups (0.46 ± SD 0.21) than non-provisioned groups (0.29 ± 0.23) (Mann–Whitney U test, U = 231, P = 0.237). I also found a positive correlation between group size and infant: adult female ratio (r = 0.338, P = 0.012, n = 54) (Figure 5). I observed 35 macaque deaths to be the result of human factors (e.g., car accident) or 2.4% of the population in 2007. This figure likely underestimates the true value, since most road accidents and other forms of mortality were probably not observed. Another human factor contributing to macaque mortality during the study was trapping. In 2007, 206 individuals or 14% of the population were trapped and removed from the population.

4-4 Public complaints and trapping

Macaque trapping has increased since the turn of the century. This increase in trapping was strongly correlated with an increase in public complaints over a period of 12 years, between 1996 and 2007 (r = 0.825, P = 0.001, N = 12). Strong correlations were also found between the number of macaques trapped and time (r_s = 0.909, P < 0.001, N = 12) and number of complaints and time (r_s = 0.839, P = 0.001, N = 12) (Figure 6), showing a clear increase in human-macaque conflict over the last 12 years.

5   Discussion

In this study, I found an estimated total macaque population of 1,228 to 1,454 individuals on mainland Singapore and other offshore islands. Approximately 70% of this macaque population lives within the main forested area in and around the NR, while the remainder of the population is found in much smaller forest fragments. I also recorded macaques in urban residential areas, several of which were new records in areas where macaques were not reported in the past, indicating that the human-macaque interface is growing in Singapore. These newly recorded sighting locations could also be due to the release of pets or macaques moving to new areas due to attraction to human settlement.

The population of long-tailed macaques now appears to be most abundant in regions near human settlements and roads, even within the NR where relatively large forested areas exist. A potential confound for this result was the possibility of differential sighting efficiency in the differing habitats. It may have been easier to

observe macaques near human environments, and more difficult in heavily forested areas. Despite this, my results are consistent with known distributions of M. *fascicularis*, as long-tailed macaques show riverine refuging behavior and tend to occur at lower densities in interior forests (Chapter I). Thus it is unlikely that sighting efficiency alone can account for the difference in distribution I observed. Clearly, *M. fascicularis* has a preference for forest edge habitats, and consequently, roads may mimic their niche preference. The human landscape, like a riverine forest is cut by alleyways (i.e., roads), creating forest edge and providing an exploitable niche for macaques. The highly modified landscape of Singapore has provided a suitable macaque niche where the nature reserves and other forest areas border human settlement. It is however important to note that I did not specifically survey macaques along the reservoir edges, which would have required separate survey effort by boat. Thus I could not gauge whether true riverine refuging behaviour along water edges was exhibited by the Singapore macaque population.

Historical and on-going human food provisioning is another factor that contributes to high abundance and distribution of macaques near human settlements. 73.5% of observed groups were accustomed to human presence and at least 54.6% of the macaque population was habituated to human provisioning to varying extents. Provisioned macaques have larger group sizes and higher infant: adult female ratios compared to non-provisioned macaques. Moreover, they are mostly concentrated on the border of human settlement where provisioning is more readily available as these macaques have learnt to associate humans as a food source, and thus they are attracted to human activity (Fuentes et al., 2008; Chapter III). It is important to note that feeding of macaques is prohibited within the NR. Moreover, the management of

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the NR does not actively provision macaque groups, which differs from the controlled provisioning of *Macaca sylvanus* in Upper Rock Nature Reserve in Gibraltar (Cortes & Shaw, 2006). Despite this effort, feeding by the public, especially outside of reserves, still occurs commonly in Singapore (M. Gumert, personal communication).

The density population density of macaques in Singapore (28.2-47.6 individuals/km^2) is considered very low in comparison to densities reported in other areas similar to the Singapore context, such as in Hong Kong (326 individuals/km^2) (Wong & Ni, 2000) and Bali (1111 individuals/km^2) (Wheatley, 1999), which can attain densities over 1,000 individuals/km^2 (Wheatley, et al. 1996; Wheatley, 1980). It is also low compared to reported island populations, for example on Pulau Penutjang off of Java, Indonesia, the density was report to be higher than 400 individuals/km^2 (Angst, 1975). The density in Singapore is also lower than that reported for more naturalistic populations (i.e., little human-macaque interface), for example in Sumatra, Crockett & Wilson (1980) surveyed 111.45 km^2 of area and found an average density of 2.98 troops and 55 individuals/km^2. Similar densities of naturalistic populations are reported elsewhere (see Fooden 1995 for a review). It is unclear what is maintaining the Singaporean macaque population from growing significantly, but it is possible that growth is minimized by human-induced mortality resulting from road accidents and trapping, in addition to natural causes of mortality.

I cannot conclude at this point, whether population density is a major driver of human-macaque conflict. Although absolute population density may not drive the human-macaque conflict; however, since there is a bias in distribution of macaques near roads and human settlement, macaques are quite conspicuous in Singapore.

Therefore, it is possible that the high visibility of macaques in Singapore gives a false impression of an unusually large and dense macaque population. Since the human population must interface with macaques in these zones on a daily basis, their perception is based on frequency of sighting rather than an unbiased assessment of the actual population size and density.

Chapter III

Macaque-human interactions and the societal perceptions of macaques in Singapore

1. Abstract

Humans and long-tailed macaques (*Macaca fascicularis*) interface in several locations in Singapore. I investigated six of these interface zones to assess the level of conflict between the two species. I observed macaque-to-human interactions and distributed questionnaires to residents and visitors of nature reserves. I observed an average of two macaque-to-human interactions per hour at the sites, which included affiliative or submissive behaviors (46.9%), aggression (19.1%), taking food and other items (18.5%) searching bins, cars, and houses (13.4%), and nonaggressive contact (2.1%). Two-thirds of interactions occurred when a human was carrying food or food cues, and one-quarter occurred when a human provoked macaques. Only 8% of interactions occurred without a clear human-triggered context. My interview showed one-third of respondents experienced nuisance problems from macaques. They had items taken from them (50.5%) and received threats (31.9%). Residents reported more nuisance problems than visitors, and their perceptions toward macaques differed. Residents were more aware of the consequences of food provisioning and that there were regulations against feeding. Residents fed macaques less and held more negative sentiments toward macaques. Nearly half of the

interviewed people held neutral attitudes toward macaques and only 26.2% of respondents thought conflict with macaques warranted urgent action. Nearly two-thirds of the respondents supported education programs to ameliorate human–macaque conflict, and less than 15% supported removing or eradicating macaques. 87.6% felt that it is importance to conserve and protect macaques. Our results show that human–macaque conflict exists in Singapore, but that it may not be severe. Human behavior is largely responsible for macaque-to-human interactions, and thus could be lessened with management of human behavior in interface zones (i.e. restrict food carrying and provocation). Moreover, my interviews shows people living in Singapore value macaques, do not wish them entirely removed, prefer education-based solutions, and consider conservation and protection of them important.

2. Introduction

In interface zones, humans and macaques have direct interactions because they utilize some of the same spaces (e.g. roads and sidewalks). A recent study by Fuentes et al. (2008) indicated that human–macaque interactions in Singapore occur most frequently when humans were carrying or offering food items, and this is similar to findings in Bali, Indonesia (Fuentes 2006a; b). In Singapore, it is an offence punishable with fining to feed monkeys within the boundaries of the nature reserves (Chapter VI). Despite this, fining macaque feeders has not eradicated the problem. For example, feeding outside of park and reserve boundaries is beyond the jurisdiction of the feeding fine. Moreover, in 2007, 157 feeders were fined inside Singapore's parks, which were the most number of fines given in any single year

since the enactment of the law (Mulchand, 2008). This inability to stop macaque feeding inside the parks entirely through punishment indicates that there may be underlying social factors contributing to the behavior of feeding monkeys that are difficult to reverse. These factors should be better understood in order to target management efforts appropriately.

In Singapore, the two major groups interfacing with macaques are park visitors and residents living near reserve borders. These two groups of people interact differently with macaques and are likely to have different perceptions about them (e.g. Elmore et al., 2007; Fellowes, 1992; King & Lee, 1987; Lucas, 1995; Strum, 1984). Residents are likely to be more disturbed by macaques, and visitors may be more amenable to having macaques living around the parks. This difference is because the costs associated with the human-macaque interface are greater for residents who must frequently interact with macaques during their daily lives. In contrast, visitors to the parks are only interacting with macaques for short periods and during their leisure time. Residents also are more likely to suffer loss or damage of property than visitors. By assessing the attitudes of people toward macaques I can study the differences in perceptions of visitors and residents. In addition, I can also obtain an estimate of the value of macaques to Singaporeans. Such information could aid my understanding of the human-macaque interface and be useful to management decisions aimed at ameliorating conflict.

In this study, I assessed human-macaque conflict in Singapore by investigating the relationship between humans and macaques. First, I studied macaque behavior towards humans and their context at six locations reported to have high macaque densities and high levels of human-macaque conflict in Singapore. Second, I

provided questionnaires to residents and visitors of the NR in Singapore. I inquired

about feeding, as well as knowledge, attitudes, and opinions about management

strategies for macaques. I tested for differences between residents and visitors in

their perceptions toward macaques. Lastly, I examined the complaint records and

media reports on macaques in Singapore and related their trends to the actual level of

human-macaque interaction and the perceptions that people have about Singapore's

macaques.

3. Methods

3-1 Study area

I identified six study areas (Figure 7a) that had high macaque densities

(Chapter II) and incidents of macaque complaints from AVA/NParks (2005) (Figure

7b). These areas were at Bukit Timah Nature Reserve and parks near or within the

Central Catchment Nature Reserve. The first site, Bukit Timah (163ha), is the most

visited nature reserve in Singapore, and is used for trekking, nature walks,

photography, cycling, bird watching, and exercise. Four other sites were MacRitchie

Reservoir Park (12 ha), Upper Peirce Reservoir Park (6ha), Lower Peirce Reservoir

Park (6 ha), and Upper Seletar Reservoir Park (15ha), which are all recreation parks

at the Central Catchment Nature Reserve, and are visited by picnickers, joggers, and

nature enthusiasts. Upper Seletar is adjacent to a 9-hole golf course that is open to

the public, and sometimes encroached by macaques.

Macaques often frequent the area surrounding Old Upper Thomson Road, a

narrow double-lane road that links Upper Peirce and Lower Peirce. Three of these

parks, MacRitchie, Lower Peirce, and Bukit Timah, have numerous condominiums

and private housing estates right at the borders of the reserve and park area

boundaries. For example, at Bukit Timah, nothing separates houses from the

designated reserve boundary and trees overhang some of the condominiums and

border within 1 or 2m of the forest edge. At MacRitchie, some houses are built along

the park border with only fenced yards separating the privately owned residential

areas from the park. Also, along Lower Peirce, only Old Upper Thomson Road

separates private houses and condominiums from the park areas, and thus macaques

easily enter the residential areas. The sixth site was along Rifle Range Road, which is

the main road linking Bukit Timah and the Central Catchment Nature Reserve, as

well as an area of frequent complaint about human-macaque conflict by pedestrians

and joggers along the road.

3-2 Observation of macaque behavior

In each of these six areas I observed how macaques behaved towards humans

between June 2nd and August 27th 2007. Observations were conducted for 2 hr at a

time, and 24 hr of data were collected at each of the six sites for a total of 144 hr.

Observations were conducted along routes that were selected because of the presence

of human settlement, high human activity, and macaques. The first author and an

assistant searched these routes for macaques and once groups were encountered,

observations began. Observers followed the macaques and recorded behaviors

macaques showed towards humans ad libitum (Altmann, 1974). When the macaque

group was lost during an observation period, the observer scanned the routes until

macaques were sighted again and resumed observation.

Macaque behaviors were classified into five main categories, with sub-categories. I recorded 1) aggressive interactions, which included a) threats, b) lunging or chasing, and b) scratching or biting. I also scored 2) the grabbing and taking of food or possessions by individual macaques and food mobbing where numerous macaques tried to grab food from a person. Other social interactions I scored included 3) affiliation and submission, 4) nonaggressive physical contact; and 5) interactions with any human structures in the environment, such as trash bins, cars, and houses. In addition to these behaviors, I recorded the context of each interaction observed. Contexts were classified into three categories: feeding, provoked, and retaliation. Feeding was when feeding or feeding cues (e.g. human carrying a plastic bag or food package) occurred during the interaction. A provoked context was when a human initiated action toward a macaque (e.g. chasing, pointing at close range, approaching closely, etc.). Lastly, behaviors were classified as a retaliation context if a macaque behavior towards human resulted from a prior action by a human to chase them away or physically advance to intervene the macaque's activity (e.g. stop a macaque from grabbing food from a trash can, entering a home, sitting on a car, etc.). Where no observable human context was observed in the interactions, I classified this as "no context". The observations were recorded as an action/reaction with only the first macaque behavior exhibited towards a human receiver and the human context in each interaction recorded. Where more than one macaque were observed in any interaction, only the behavior of the nearest macaque to human receiver was recorded; with the exception of mobbing, where more than one macaque were clearly interacting closely with the human receiver at the same time.

3-3 Questionnaire survey

The survey questionnaire (in English) included both objective and subjective questions about the opinions, knowledge, and attitudes toward macaques by residents and visitors to the parks. 519 people participated in the survey. 393 surveys were administered to park visitors from all areas except Rifle Range Road. 126 surveys were administered to residents living on the borders of Bukit Timah, Lower Peirce, and MacRitchie. Visitors were surveyed by volunteers and staff of National Parks Board (NParks), and were approached and asked to answer a series of questions. Interviewers were stationed along the same routes used for behavior data collection and they approached visitors met along the route. Residents were surveyed by interviewers that went from house-to-house in residences along park borders. Each questionnaire survey was conducted verbally and answers were recorded by the interviewer in the presence of the participant.

3-4 Complaints and media portrayals

I obtained and compiled the records of unsolicited complaints received by email from the NParks (N = 529) between January and October 2007. Each complaint was classified according to its context. Contexts were, (1) "stealing" food and/or belongings, (2) entering and/or damaging property, (3) attacks, (4) general nuisance, and (5) macaque sightings. In addition to this, I also compiled media headlines from Singaporean newspaper articles between 2004 and 2008 (N = 546). Each headline was classified according to whether it conveyed positive, negative, or neutral connotations toward macaques. Negative connotations included words such as "rob", "steal", "thieving", "aggressive", "nasty", "harassed", "havoc", "nuisance",

"threat", "torment", "mayhem" or conveying message of macaque as "obstructing traffic", "stopping passersby", or "causing a vehicle crash". Positive or neutral connotations included depicting macaques as "not a threat to park visitors", "man and not animals as culprits", and "feeding that harms macaques", and general discussions about macaques.

3-4 Data analysis

I calculated the proportion that each behavioral category represented of the total ad libitum data set as well as the rate of observed interaction per hour of observation. I used a Chi-Square test to test whether there was variation in the proportion of interaction types among the six study sites to determine if there might be any differences between study sites in the type of macaque behavior observed. In addition, I used Chi-Square tests to test for differences in frequency between the different types of macaque behaviors. This allowed us to determine if certain types of macaque-to-human interactions were more common than others. Lastly, I used independent-samples t-tests to test whether more macaque behaviors occurred in human-triggered contexts than in context without any clear human instigation.

All of the questionnaire survey data were checked for completeness and unclear answers were removed from the analysis. No forms were completely discarded, as a survey needed only to contain at least one complete answer to a question to be useable. The survey answers were categorized and the percentage of each type of answer was calculated. An arcsine transformation was applied to normalize the percentage data, and I used independent-samples t-tests to determine whether there were any significant differences between the responses of residents

and visitors for all of the survey questions. Chi-Square tests were used to test for significant differences between (1) the types of nuisance problems experienced by respondents, (2) attitudes toward macaques, (3) attitudes toward macaques among those not ever harassed, (4) attitudes toward macaques among those who have been harassed (5) context of complaints received in 2007, and (6) rationale for conserving macaques.

I also compared the following subsets from the questionnaire data using independent-samples t-tests: (1) among those who knew about the fine for feeding macaques, were compared how many fed macaques and how many did not; (2) among those who expressed inclinations to feed macaques, I compared how many thought macaques had enough natural food resources and how many did not think they had enough; (3) among those who thought that urgent action is needed, I compared how many supported manipulation of the macaque population and how many supported education on co-existence; (4) I assessed if there were differences in the respondents' attitude toward macaques (i.e. positive, negative, or neutral), depending on whether someone had received harassment or not; (5) among those who indicated an urgent need for action, I compared how many had received harassment and how many had not; and (6) among those who indicated support for direct manipulation of the macaque population, I compared how many had received harassment and how many had not. I determined whether the proportion of positive headlines on macaques in Singapore's media was significantly less than the proportion of neutral and negative headlines combined by using independent t-tests. All analyses were conducted using the Statistical Package for the Social Sciences

version 13.0 (SPSS Inc. Chicago, IL). Statistical significance for all tests was set at $P < 0.05$.

4. Results

4-1 Occurrence and context of macaque behavior

A total of 292 occurrences of macaque behaviors towards humans or human-made substrates were observed during the 144 hr of observation (Table 2). The rate of macaque behavior was 2.03±SD 0.45 interactions per hour. The frequency of behavior differed among the six observation sites (Chi-Square test: $\chi^2 = 104.4$; df = 20; $P = 0.001$). Affliliative/submissive gestures were highest at Upper Seletar (65.6%), Lower Peirce (59.5%), and Rifle Range Road (57.5%). Grabbing or taking human possessions were highest at Upper Peirce (28.9%), MacRitchie (23.5%), and Bukit Timah (22.5%). Lunging and chasing behavior were highest at Upper Peirce (13.4%) and MacRitchie (16.5%). House, bin, and car raiding behavior were most common at Bukit Timah (32.5%) and Rifle Range Road (17.3%). Mobbing behavior was only observed twice, once at Rifle Range Road, and once at MacRitchie. Physical contact without aggression occurred at three of the six sites-Upper Peirce, MacRitchie, and Bukit Timah.

The distribution of types of macaque behavior towards humans was not uniform (Chi-Square test: $\chi^2 = 382.1$; df = 7; $P < 0.001$). The most common was affiliative/submissive (46.9%), followed by grabbing or taking human possessions (17.8%), threats (9.9%), lunging or chasing (9.2%), physical contact without aggression (2.1%), and mobbing (0.7%). No bites or scratches (0%) were observed

during this study. Interaction with the human environment contributed to 13.4% of observed interactions and involved mainly searching of cars and trash bins.

Macaque behavior towards humans occurred mainly in the context of feeding, as nearly two-thirds of all interactions were related to food or food cues. 65.5% of interactions observed in this study occurred in the context of direct feeding or reaction to feeding cues. 6.3% of the behaviors observed were in the context of human provocation, and 20.3% of interactions were in the context of human retaliation. Only 7.9% were in a context with no clear influence by the human target, and this was significantly less than the three human-triggered contexts combined (independent-samples t-test: t = -8.0; df = 10; $P < 0.001$). Moreover, all behaviors in this unprovoked context were affiliative/submissive. Overall, most interactions (85.8%) were the result of direct conflict over food and/or space.

4-2 Human reports on interactions

I asked whether people ever experienced a nuisance problem from macaques in the form of a yes/no question. I found that 35.5% (N = 512) of interviewed respondents reported having experienced some form of nuisance. I further asked what kind of nuisance problems they experienced. I found that 50.5% reported having had items taken by macaques. In addition, 31.9% reported being threatened, chased, or followed, 10.5% were bitten or scratched, and 7.1% received property damage from macaques. The types of nuisance problems experienced were not uniform across sites, and the taking of food or other items was the most common type of nuisance (Chi-Square test: $\chi^2 = 589.6$; df = 2; $P < 0.001$).

I also found differences between residents and visitors. It was reported that 68.3% of residents and 24.4% of visitors experienced nuisance problems, and this difference was significant (independent-samples t-test: t = 5.942; df = 180; $P <$ 0.001). The percent of residents (29.1%) and visitors (34.4%) who experienced threats (independent-samples t-test: t = 0.820; df = 180; P = 0.4132) and or having had items taken from them (residents: 53.5%; visitor: 47.9%, independent-samples t-test: t = 0.877; df = 180; P = 0.3816) was not found to be significantly different. Visitors (17.7%) did report significantly more experiences of being bitten or scratched by macaques than residents (2.3%) (independent-samples t-test: t = 53.407; df = 180; P = 0.0008). Only residents experienced property damage, which amounted to 15.1% of the nuisance problems reported.

I asked people what they thought were the causes of macaque-to-human interaction, and provided four possible answers. I found that the majority of people perceived the cause to be the result of attraction to food (58.6%). The three others causes were the macaques being provoked by humans (18.5%), being playful (17.8%), and being aggressive (5.1%). The percent of residents (71.3%) who thought that nuisance problems were caused by macaques attracted to food was significantly higher than visitors (53.8%) (independent-samples t-test: t = 0.5178; df = 409; $P <$ 0.001). In addition, more visitors (20.9%) than residents (9.6%) thought that problems were owing to macaques being playful (independent-samples t-test: t = 2.721; df = 409; P = 0.0068). The percent of visitors (4.7%) and residents (6.1%) that thought that macaques were aggressive (independent-samples t-test: t = 0.580; df = 409; P = 0.5625) or provoked by humans (independent-samples t-test: t = 1.806; df = 409; P = 0.0717) was not found to be significantly different in this study.

4-3 Human reports of macaque feeding

In my survey, I queried people about their behavior and knowledge on the feeding of macaques, and its influence on human–macaque conflict. I found that 14.2% of all respondents reported having fed monkeys in the past, and that 16.8% reported that they would be interested in feeding the macaques in the future. 74.6% of all respondents knew that they were liable to be fined if they were caught feeding monkeys, and thus there was high awareness of the law. I also found clear differences between visitors and residents in attitudes and knowledge about feeding. I found that significantly more visitors (16.4%) than residents (7.3%) reported to have fed the macaques at some time (independent-samples t-test: t = 2.532; df = 505; P = 0.0116). I also found that significantly more visitors (20.1%) than residents (6.6%) reported being more interested in feeding macaques in the future. Lastly, I found that residents (80.3%) were significantly more aware of the feeding fine than visitors (72.8%) (independent-samples t-test: t = 3.093; df = 371; P = 0.0021).

I also tested if people with knowledge about the fines reported different behavior than those not knowledgeable about the fines, in order to assess the impact of fining on feeding behavior. Among those who knew about the fine for feeding macaques, the percent that reported to have fed monkeys in the past or an interest to feed monkeys in future (N = 556, 15.0%) was significantly lower than those who indicated that they did not know about the fines (85.0%) (independent-samples t-test: t = 14.515; df = 498; P < 0.0001). I did find that 33.3% of those who were inclined to feed macaques claimed they did not know about the fine. 79.2% of all respondents (N = 392) thought that the feeding ban was effective at reducing monkey feeding, but

N = 544 (11.2%) questioned the effectiveness of enforcing it. These skeptical respondents expressed the need for heavier fines, more enforcement, or stronger education efforts. 57.3% of respondents felt that macaques had enough food in the forests and did not require additional human provisioning, and only 25.9% of such respondents reported having fed or having an interest to feed the macaques. In contrast, 65.0% of those inclined to feed monkeys thought the macaques did not have enough natural food sources, and 47.1% of these respondents reported to have fed or to have an interest to feed macaques. These two groups differed significantly in the amount of feeding or interest in feeding reported (independent-samples t-test: t = 4.788; df = 493; $P < 0.0001$).

4-4 Attitudes about macaques and their management

In my questionnaire, I investigated the attitudes that people have toward Singapore's macaques. I provided five options for them to answer: (1) strong liking for macaques; (2) mild liking for macaques, (3) strong dislike for macaques; (4) mild dislike for macaques, and (5) neutral about macaques. Both strong and mild like were grouped as a positive attitude and both strong and mild dislike as a negative attitude. I found 47.4% of interviewees held neutral attitudes, 32.9% held positive attitudes, and 19.7% held negative attitudes and that attitudes were not uniformly distributed (Chi-Square test: $\chi^2 = 58.0$; df = 2; $P = 0.0001$). I also found differences between visitors and residents in attitude. Visitors viewed macaques more positively than residents, because the percent of visitors that reported a positive attitude for macaques (36.8%) was significantly higher than residents (21.0%) (independent-samples t-test: t = 3.386; df = 505; $P = 0.0008$). Moreover, the percent

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of visitors that reported a negative attitude (15.7%) was significantly lower than residents (32.2%) (independent-samples t-test: t = 4.012; df = 505; $P < 0.001$). I could find no significant difference in neutral attitudes toward macaques between visitors and residents (independent-samples t-test: t = 0.136; df = 505; $P = 0.8921$).

I questioned people on whether they were aware of human–macaque conflict in Singapore and whether they thought any urgent management was needed. I found that 66.2% of all respondents reported being aware of conflict between humans and macaques. Residents (84.8%) were significantly more aware than visitors (59.9%) (independent-samples t-test: t = 5.057; df = 394; $P < 0.001$). 26.2% of all respondents reported thinking that an urgent management program was needed.

I further asked people what measures they thought should be taken to manage macaques. Interviewees were provided with five choices: (1) complete eradication of macaques from Singapore, (2) population reduction, (3) removal of nuisance macaques, (4) keeping nuisance macaques from urban areas, or (5) education on co-existence with macaques. I found that the majority (63.6%) of people interviewed thought that education on coexistence with the macaques would be the most important measure if any were to be taken. The next popular option (21.1%) was keeping macaques or nuisance monkeys from park borders and urban areas. Only 10.9% felt that it was important to reduce the population, 2.2% were for removal of nuisance macaques, and 2.2% thought that macaques should be completely eradicated from Singapore. In addition, of those reporting a need for urgent action, 47.2% supported direct manipulation of the macaque population (i.e. reduce or eradicate) and 52.8% supported education on coexistence. I could not find any

significant difference between these two perspectives (independent-samples t-test: t = 1.209; df = 501; P = 0.2274).

I investigated the differences between residents and visitors in their opinions on resolving human–macaque conflict. I found that significantly more residents (21.5%) than visitors (7.6%) supported reduction of macaque population (independent-samples t-test: t = 4.309; df = 501; P < 0.001) and removal of nuisance macaques (residents 5.8%, visitors 1.0%) (independent-samples t-test: t = 3.170; df = 501; P = 0.0016) and significantly more visitors (67.3%) than residents (52.1%) indicated education on co-existence with macaques (independent-samples t-test: t = 3.953; df = 501; P = 0.0001). Residents and visitors who indicated eradication of macaques (residents 0.8%, visitors 2.6%) and keeping nuisance macaques out of urban areas (residents 19.8%, visitors 21.5%) did not differ significantly (independent-samples t-test: t = 2.2; df = 501; P = 0.2366, t = 21.1; df = 501; P = 0.5235). I also found that the percent of residents who stated a need for more urgent action and supported more immediate management methods (64.3%) were higher than visitors (33.8%) (independent-samples t-test: t = 3.418; df = 125; P = 0.0009). Overall, 87.6% of total respondents believed that macaques should be conserved and provided more protection, and this was not found to be significantly different between visitors and residents (independent-samples t-test: t - 0.276; df = 344; P = 0.7823).

Out of 112 respondents who provided subjective answers to the rationale for conserving macaques, 38.4% reported that macaques play an important role in balancing the forest ecosystem, 26.9% reported that macaques have an intrinsic biodiversity value, 20.9% reported that macaques should be protected for welfare

reasons, 8.8% reported their esthetic and entertainment value, 2.7% reported religious reasons, and 2.3% reported other reasons. The rationale for conserving macaques was not uniformly distributed (Chi-Square test: $\chi^2 = 63.5$; df = 5; $P < 0.0001$). Questions and responses to the interviews were compiled and summarized in Table 3.

4-5 Experience and attitudes towards macaques

I investigated if people that had negative experiences with macaques were more likely to show negative attitudes toward them, and whether they were more supportive of urgent action being taken. I found that responses among people that had been harassed were not uniformly distributed. 36.1% indicated positive attitudes toward macaques, 23.2% indicated negative attitudes, and 40.7% indicated neutral attitudes (Chi-Square test: $\chi^2 = 9.541$; df = 2; $P = 0.0085$). Responses among those not ever harassed were also not uniformly distributed. 30.3% indicated positive attitudes toward macaques, 17.5% indicated negative attitudes, and 52.2% indicated neutral attitudes (Chi-Square: $\chi^2 = 60.436$; df = 2; $P = 0.0001$). People who had experienced harassment were not found to be significantly more likely to indicate a difference in their overall attitude toward macaques, whether positive (independent-samples t-test: t = 0.820; df = 460; $P = 0.4128$) or negative (independent-samples t-test: t = 1.275; df = 460; $P = 0.2029$) but neutral attitudes toward macaques were significantly lower for those who had received harassment (independent-samples t-test: t = 2.006; df = 460; $P = 0.0455$). Therefore, past experiences with macaques did not seem to be strongly related to a person's general attitude toward them.

In contrast, I did find that past experience affected people's opinions on management strategies. First, those who received harassment (N = 512) were significantly more likely to indicate an urgent need for action than those who had not received harassment (N = 530) (33.5% compared with 20%) (independent-samples t-test: t = 3.515; df = 510; P = 0.0005). Secondly, people that had received harassment were not found to be more likely to support direct manipulation of the macaque population (49.9%) than alternative strategies (51.1%) (t-test: t = 0.297; df = 181; P = 0.7669). However, when I compared residents and visitors, I found that residents that had received harassment supported direct manipulation of the macaque population (69.8%) significantly more than visitors that had (30.2%) (independent-samples t-test: t = 5.336; df = 180; P < 0.001).

4-6 Complaints and media headlines

I compiled complaint records and media headlines to assess the contexts that human–macaque conflict occurred in and how the media has portrayed the conflict. To investigate complaints, I examined feedback emails to NParks (N = 529) that were received between January and October 2007 (Table 4). From this sample, I found five contexts in which complaints occurred. I found that 37.9% of complaints were related to having food and belongings taken, 27.6% were about macaques that had entered or damaged property, 10.3% were perceived as attacks, 6.9% were general nuisance complaints, and 17.3% were simply reports of monkey sightings that had concerned the informant. These complaint contexts were not uniformly distributed (Chi-Square test: χ^2 = 9.4; df = 3; P = 0.002). I also assessed 47 media headlines from Singaporean newspapers (Table 5) between 2004 and 2008. I found

that 20 (42.6%) articles contained words conveying negative connotations to macaques, that 6 (12.7%) contained positive connotations, and 21(44.7%) contained neutral connotations. Positive headlines on macaques in Singapore's media were significantly less than neutral and negative headlines (Independent-samples t-test: t = 5.224; df = 46; $P < 0.0001$).

5. Discussion

5-1 Macaque behavior towards humans in Singapore

My observations of macaque behavior towards humans in high interface areas of Singapore indicated which types of interactions were most common and the contexts in which these interactions occurred. Nearly half of all behaviors observed were affiliative or submissive, about a fifth involved taking or grabbing of food or other items possessed by people, and approximately a ninth involved macaques accessing houses, refuse bins and cars. Nearly two-third of all behaviors occurred when people were carrying food or food cues (i.e. bags or packages), and around one-quarter of all interactions occurred directly from human provocation or retaliation. Only 8% of all interaction had no clear provocation from humans, indicating that potentially some simple alterations in human behavior around macaques (i.e. not carrying food or provoking macaques) could possibly reduce up to 90% of all behavior that long-tailed macaques direct toward humans in Singapore.

Occurrence and frequency of interaction types differed among the six different study areas. A variety of factors may influence how macaques and humans interact. These could include features of the location, as well as the history of interaction between people and macaques at a site. Interaction may vary in response to the

degree of overlap in physical space, macaque hunger, thirst, and/or changes in season (e.g. fruit availability). Additionally, macaques may be more motivated to interact with people based on their prior experiences surrounding feeding, harassment, and/or other contact with humans (Alexander & Roth, 1971; Anderson et al., 1977; Eaton et al., 1981; Erwin, 1977; Erwin & Erwin, 1976; Fellowes, 1992; Southwick, 1967; Southwick, 1969). Overall, our results suggest that the majority of macaque behavior towards humans seemed related to locating and obtaining food. This result has also been found in numerous other countries where high levels of macaque interface occur (Hong Kong: Fellowes, 1992; Bali: Fuentes & Gamerl, 2005; Fuentes et al., 2005; Malaysia: Norma-Rashid & Azarae, 1992; Gibraltar: O'Leary & Fa 1993; Fuentes, 2006a; India: Pirta et al., 1997; China: Zhao, 1994; Zhao, 1996).

My investigations using interview surveys, complaints records, and media headlines indicated the common types of nuisance problems received by people, as well as attitudes and perceptions held about macaques. I found that taking of food items or belongings, receiving aggression by macaques, and experiencing property damage to fruit trees and ornamental gardens were the most common types of complaints from people interfacing with macaques. Only about a third of respondents had reported being harassed by macaques, and residents reported more nuisance problems than visitors. The percent of residents and visitors who experienced common nuisance problems like threats and taking of items were not found to differ, but visitors reported more bites and scratches, and only residents experienced property damage. This demonstrates that each of these groups face different challenges in areas of human–macaque interface.

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No bites or scratches were observed to occur in this study or by another recent study in Singapore (Fuentes et al., 2008), although 10% of interviewed respondents indicated being bitten or scratched. In India, it is estimated that 100 people were being injured by monkeys every day, of which many were bites (Malik, 2001). In Gibraltar, UK, 248 bite cases were reported in a 9-year period (Fa, 1992). In the temple monkey forest of Padengtegal in Bali, Indonesia, 48 bites were observed within 6 weeks of observation (Fuentes & Gamerl, 2005). Incidences in Singapore appear to be much lower, although rigorous comparisons across commensal regions are limited without a thorough assessment of the number of people and macaques interfacing and amount of area in which they interface.

In Singapore, I found a rate of 2.03 interactions per hour. This finding is much lower than in tourist areas in Gibraltar, where the interaction rates were found to be 99.6 (O'Leary & Fa, 1993) and 30.6 interactions per hour (Fuentes, 2006a). This difference is likely because the interface in Gibraltar occurs in a small area densely packed with tourists and macaques, and people come to the area to directly interact with and feed the monkeys. The rate of aggressive interaction found in this study was 0.39 interactions per hour. This finding is lower than the rate of 4.67 aggressive interactions per hour in the temple monkeys of Bali (Fuentes, 2006b) but slightly higher than the urban macaques of Hong Kong (0.26 per hour) (Fellowes, 1992). It appears that tourist site monkeys may have higher interactions rates than urban macaques.

5-2 Macaque feeding

Provisioning can alter the behavior of macaques and lead to higher levels of interaction with people (Edington & Edington, 1986; Wheatley et al., 1996). It is likely that historical food provisioning has been one factor contributing to the overlap between humans and macaques in Singapore. About a sixth of total respondents indicated that they were inclined to feed macaques, but it is worth noting that the proportion may be under-represented owing to reluctance by some respondents to admit to feeding macaques for fear of repercussions (i.e. fining by park service authorities that were administering the test). 75% of respondents indicated that they knew about the fine for feeding macaques, and a larger proportion of residents were more aware of the fine than visitors.

Residents were less likely to feed macaques than visitors, and I speculate that this is owing to more awareness of the feeding fine and better knowledge about the potential of their actions to exacerbate nuisance problems, owing to education efforts by Singapore's National Parks Board (NParks). Another factor is that residents are more influenced by the results of feeding and thus have greater incentives to avoid feeding in order to ameliorate human-macaque conflict. However, this is not to say that residents do not contribute to macaque feeding, and the minority of feeders may still be attracting macaques to remain in residential areas despite their neighbors' efforts. Visitors also feed macaques in residential areas. For example, they provide food from cars along roads and lay out food in areas where macaques frequent around residential areas, attracting them more to these areas. Therefore, despite residents' efforts, visitors also contribute to keeping macaques in residential areas. Consequently, fining efforts need to expand beyond park borders to protect residents

affected by macaques and education efforts on the feeding ban and negative impacts of feeding on macaque ranging patterns should continue until feeding is eliminated.

As noted by Lucas (1995), I found that the motivation for humans to feed macaques is partly related to the notion that macaques do not have enough food in the forests, although the majority of feeding is likely for hedonic reasons (i.e. people enjoy it). The feeding ban has achieved some success, and 80% of the people interviewed perceived the feeding ban as being effective in curbing feeding. Also, when compared with past reports on the levels of feeding it appears that feeding has lowered from the 1980s, a time when visitors visited the parks to feed macaques for recreation (Lucas, 1995). A small percentage of the respondents questioned the effectiveness of enforcing the feeding ban. These people expressed the need for heavier fines or alternative measures though education efforts, and their input is important to note because their comments reflect the reality that feeding still occurs in and around the reserves and parks.

5-3 Human-macaque conflict in Singapore

The conflict between long-tailed macaques and people in Singapore has been highlighted as an escalating issue by the media and management authorities, and therefore has become an issue of public interest to Singaporeans in recent years (Chapter I). Overall, my results and others (Fuentes et al., 2008; Jones-Engel et al., 2006) on interactions between human and macaques have shown that Singapore might have one of the most benign human-macaque interfaces in the world. Therefore, the human-macaque conflict situation may be less severe than is depicted by media and management reports. Moreover, the majority of interview respondents

do not seem to show any great animosity toward macaques, and the majority of people prefer management strategies that do not involve the removal of macaques. This situation could reflect the success of Singapore's efforts to manage their human-macaque interface over the past several years through educational and enforcement methods. Alternatively, it could also represent something intrinsic about the macaques, people, or habitat of Singapore. These questions make it critical to continue to increase my understanding of the human-macaque interface in Singapore in order to gain information that could later be used to aid people in other regions, who are attempting to understand and ameliorate their own human-macaque conflicts.

The human-macaque conflict situation directly affects only a small proportion of the Singaporean population, and is mainly affecting the lives of people that live on the fringes of forest patches. Despite this, it remains a challenge for management authorities to sufficiently address and curtail macaque nuisance problems in a way that satisfies the small percentage of affected persons, while also benefiting the general public's interest in their natural heritage commonwealth and maintaining a healthy and stable macaque population. My interview survey showed a strong support for humane management options like conflict resolution through education and little support for the removal and eradication of macaques. These findings should be useful to management authorities in deciding how to best approach Singapore's human-macaque conflict, by understanding the perspectives of people living with macaques. Moreover, management authorities must be careful to not allow biased press reports and media depictions of nuisance macaques generated from the complaints of a small proportion of the affected people living with macaques send

the wrong information about the severity of human-macaque conflict in Singapore. Singapore indeed suffers from problems associated with humans living in close proximity with macaques, but the results of my study indicate the situation is manageable and there is ample public support for maintaining a macaque population.

Chapter IV

Diet, activity, habitat use, and ranging of two neighboring groups of food-enhanced long-tailed macaques (*Macaca fascicularis*)

1. Abstract

I conducted observations of two neighboring groups of food-enhanced long-tailed macaques (*Macaca fascicularis*) over a period of one year. I examined their diet, behavior, habitat use, and ranging and how within-population variability reflected differential utilization of anthropogenic food resources. The group that consumed more anthropogenic food spent less time feeding on wild fruits and flowers, less time resting, and more time locomoting. They used forest habitats less often, and had a larger total home range and mean monthly home range. Some of these results contrasted with previous studies of food-enhanced primates which reported that food-enhancement resulted in smaller home ranges, shorter daily ranges, less time traveling and feeding, and more time resting. These contrasting patterns may relate to the nature of anthropogenic foods. In most studies of food-enhanced primates, anthropogenic food resources were abundant and concentrated but the macaques in this study used anthropogenic foods mainly from a few refuse sites where they had limited access, and from dispersed and irregular human provisioning. The group consuming more anthropogenic food therefore showed more spatially

dispersed feeding activity and home range use, an effect that was likely further enhanced by lower natural food resource availability within their home range. The Singapore macaque population shows small-scale variability in feeding and ranging behavior, contributing to the complexity of their adaptive variability in a human-altered habitat. My findings could have important implications for mitigating human-macaque conflict as measures applied at a higher spatial or population level may achieve highly inconsistent results, intensifying the challenges for wildlife managers.

2. Introduction

Considerable ecological variability is found in wild primate species (Chapman & Rothman, 2009; Strier, 2009). Intra-population variation in ecology has been found between primate groups in highly heterogeneous natural and human-altered habitats (e.g. El Alami et al., 2012; Ganas et al., 2004; Hanya et al., 2008; Harris & Chapman, 2007; McKinney, 2011; Potts et al., 2011). Food resource availability and distribution are important factors determining such ecological variations in primate species (Struhsaker, 1997; Wrangham, 1980).

Due to increasing human population pressure and natural habitat loss, many primate populations inhabit human-influenced landscapes where they have access to anthropogenic food that are often palatable, energy-rich, easily digestible, spatially clumped and abundant (Chapter I). Where food resources are abundant and concentrated, individuals can reduce travel cost and food competition (Chapman et al., 1995; Gillespie & Chapman, 2001; Janson & Goldsmith, 1995), adopting foraging strategies that minimize foraging time as opposed to maximizing energy

intake (Hixon, 1982; Schoener, 1971). The inclusion of human food sources has significant effects on the ecology of many primate species (Chapter I). There are some exceptions to these trends, however. For example, McKinney (2011) found that food-enhanced capuchins maintained a much larger territory than wild conspecifics, with a similar activity budget. Campbell-Smith et al. (2011) found that crop-raiding orangutans traveled further on days when they raided crops than on days when they consumed only wild fruits. Similarly, Hockings et al. (2012) reported that chimpanzees increased travel and feeding time on days when they crop-raided. These various patterns highlight the complexity of primate ecological responses to food enhancement, which may depend on species and individual group and site conditions (Hockings et al., 2012; McKinney, 2011). Food-enhanced primates provide opportunities to examine possible adaptive variability in their behavior and ecology, which is expected to differ depending on how they exploit anthropogenic food resources.

In Singapore, long-tailed macaques occur in a variety of natural habitats including primary, secondary, freshwater swamp, and mangrove forests, but are found mostly along forest edges, where they are habituated to source for human food (Chapter II). Forest fragmentation, degradation, and loss, coupled with the availability of anthropogenic food resources in human altered habitats; create a situation in which the monkeys' behavior and ecology is significantly influenced by anthropogenic factors (Chapter 1).

In this study, I aimed to investigate how within-population variability in activity, habitat use and ranging reflects differential utilization of anthropogenic food resources. I compared two groups of long-tailed macaques with partially overlapping

home ranges and different levels of anthropogenic food exploitation, thus reducing the effects of uncontrollable environmental and ecological factors that may confound comparative studies between sites (Bicca-Marques, 2003; Butynski, 1990; Chapman & Chapman, 1999). I tested predictions that the group utilizing more anthropogenic food resources, compared to the group utilizing less anthropogenic food resources would: (1) exhibit dietary patterns consisting of less wild food resources, that is, fruits, flowers and leaves, and including a lower diversity of total and mean monthly food plant species consumed; (2) exhibit an activity budget typical of higher food enhancement, that is, more resting, less feeding and less locomotion; (3) use more urban/edge habitats compared to forest habitats; and (4) exhibit ranging patterns typical of higher food-enhancement, that is, smaller home ranges and shorter daily ranging distances. A better understanding of variable responses to anthropogenic food resources is important to guide the implementation of effective human-macaque mitigation measures.

3. Methods

3-1 Study area

This study was conducted at the Upper Seletar Reservoir Park situated within the Central Catchment Nature Reserves of Singapore (Figure 8).The park's borders include the Upper Seletar Reservoir, a divided highway, a golf course and driving range and a military firing range used regularly by military personnel. A two-lane road extends from the highway on the east to the western limits of the park. Regular visitors to the park include mainly golfers, anglers and joggers. Large school groups also visit the park occasionally for day excursions.

The vegetation within the study area consisted of a matrix of young and mature secondary forests and freshwater swamp forests. Along the edge of the forest reserves and buffering the road and urban park areas were manicured grass patches, with native and non-native trees planted at regular intervals for shade and aesthetic effect.

3-2 Data collection

I identified two groups of macaques based on observations in 2007, as part of a population study of long-tailed macaques in Singapore (Chapter II) which included an estimation of the macaques' habituation to humans and utilization of anthropogenic food resources. I observed that the two study groups received provisioning from humans and also exploited anthropogenic food resources from refuse sites. I observed the "high anthropogenic" group more frequently in urban areas where it fed more on anthropogenic resources compared to the "low anthropogenic" group. The groups were similar in size, with a range of 19 to 25 individuals in the "low anthropogenic" group and 21 to 30 individuals in the "high anthropogenic" group. I selected these groups for more detailed studies (also see Sha & Hanya, in press).

I conducted observations of the two groups each month over a one-year period (June 2011 to May 2012). I observed each group for three randomly chosen full days per month. I observed the "low anthropogenic" group in the first half of the month and the "high anthropogenic" group in the second half of the month. I logged a total of 398 hr of observation (mean ± SD: 11.1 ± 2.2 hr per observation day and 31.6 ± 3.4 hr per month) on the "low anthropogenic" group and 410 hr (mean ± SD: 11.4 ±

1.9 hr per observation day and 34.2 ± 2.6 hr per month) on the "high anthropogenic" group.

On each observation day, myself and an assistant located a macaque group at their sleeping site at dawn and followed the group till dusk. I recorded all relevant data while the assistant kept track of the movements of the macaques, recorded location data and marked feeding trees for identification. I used scan sampling (Altmann, 1974) at 15-min intervals to record activity (rest, locomotion, and forage/feed, further divided into feeding on natural and anthropogenic food sources) and habitat use (urban/edge and forest). I defined resting as any form of inactivity, with the animal in a stationary, sitting, standing or lying position, with or without eyes shut. I defined forage/feed as eating or manipulating food items. I defined locomotion as progressive movement from one location to another, not followed by foraging or feeding behavior within 3 sec. If foraging or feeding occurred within this time, I classified it as such. I distinguished urban and edge habitats (roads, concrete buildings, grass patches, and planted trees on these patches) from forest habitats consisting of forested areas with continuous tree canopies (Figure 9). I conducted scans on macaques that were within sight, up to a maximum of 5 min, and from a left to right or clockwise direction to avoid repeated counts. The mean number of individuals per scan was 23.3 ± 4.2 for the "high anthropogenic" group and 20.8 ± 3.9 for the "low anthropogenic" group. I recorded group location at 15-min intervals using a Geographic Positioning System (Trimble™ Recon, Trimble Navigation Limited).

To quantify natural resource availability, I set up 36 plots measuring 20 m x 20 m within the two home ranges and tagged trees with diameter at breast height (DBH)

> 5 cm. The plots included young secondary forest, mature secondary forest, and swamp forest, proportionally representing the habitats within the two home ranges. The approximate natural habitat type coverage of the "high-anthropogenic group" was 40% young secondary forest, 45% mature secondary forest, and 15% swamp forest and for the "low-anthropogenic group" was 40% mature secondary forest and 60% young secondary forest. Each month, I monitored phenology of trees in my plots by scoring fruits, flowers, and young leaves as absent or present.

Anthropogenic foods came from two sources, refuse bins and direct provisioning. The home range of the "high anthropogenic" group ranged included one metal bin (100 L), two large wheelie bins (660 L), and two small plastic bins (60 L) used by the golfing canteen and shop while the "low anthropogenic" group contained two fixed metal bins. The metal bin and wheelie bins were cleared daily, usually at about 8 to 9 am, while the plastic bins were cleared irregularly at the discretion of the canteen and shop owners, often only when they were full. I checked these sites once in the morning before commencing group follows, and once at noon, scoring the number of refuse sites with exposed waste. These timings followed long-term observations of the macaques' urban foraging patterns. Macaques have been observed to regularly visit these sites as part of their first feeding activity in the mornings, after which they would enter the forest, emerging again in the afternoons to visit the refuse sites, entering the forests again, before returning to their sleeping sites at the forest edges in the evenings. The morning checks accounted for refuse that was left over from the previous evening, as the park remained opened throughout the night. The afternoon checks accounted for refuse accumulated after clearance of the refuse bins in the mornings. Exposed refuse included any refuse

items that were not contained and were retrievable by macaques, including styrofoam food boxes, plastic food packages, and bits of food items in or around the refuse bins. As it was difficult to quantify the actual amount of refuse, I scored only for absence (0) or presence (1). The macaques inspect carefully any form of refuse items, even if they contained little or no food.

Park visitors who directly provisioned the macaques either deposited food items at the side of the road or threw them to the macaques. Food provisioning occurred more frequently when macaques were within sight of visitors in urban areas and this creates a bias in attempts to quantify provisioning as an independent factor. Moreover, it was difficult to quantify food items that were thrown by the side of roads or into forest edges, as these occurred in different locations and were not always directly observable. Instead I used an indirect measure based on human and car traffic, as macaques responded to traffic as if they associated it with provisioning; often approaching cars that stop by the roads (Fuentes et al., 2008; Chapter III). I conducted scans at 1hr intervals at a predetermined point within each group's urban home range, to access human and car traffic data, noting the number of humans and the number of cars. I was able to collect these data concurrently with macaque follows as the macaques were never more than 200 m from the forest edge, allowing one observer to break off the macaque follow to conduct the traffic scan.

3-3 Data analysis

I calculated home ranges as Minimum Convex Polygons (MCP), fixed mean method using "Home Range Tools" for ArcGIS® Version 1.1 (Rodgers et al., 2007) and Geographic Information System (ESRI ArcGIS™ 8.3, Environmental Systems

Research Institute, USA 2005). I used 100% MCP to represent the home range and corrected for areas of obvious non-usage, for example large water bodies.

The MCP method generally results in an overestimation of home ranges (Harris et al., 1990; Kenward, 2001; White & Garrott, 1990) but I chose this method for my between group comparison, as the simplified algorithm is less limited by statistical assumptions (Lehner, 1996; Powell, 2000) and provides a better representation of the total extent of areas used, including all point locations in which macaques were found. I measured daily travel distance by summing straight line distances between sequential GPS points.

I used the Shannon-Wiener Diversity Index (Pielou, 1974) to examine (1) plant species diversity within the two home ranges and (2) plant species diversity in each group's diet. I calculated the diversity index H using the formula:

$$H = -\Sigma\, pi \cdot \log pi$$

where H ¼ Shannon-Wiener Index of diversity, pi ¼ the proportion of individuals of species i. Higher H values indicate higher species diversity. I computed indexes for plant species diversity and food plant species diversity for each group over the entire study period, as well as monthly indexes for food plant species.

I used Morisita's Index of Dispersion (Id) (Brower et al., 1998) to examine how spatially clumped the two groups were in (1) home range use, (2) feeding activity, (3) feeding activity within urban/edge habitats, and (4) feeding activity within forest habitats. I conducted these analyses by dividing each home range into 20 m x 20 m grid squares and overlaid GPS locations of the relevant data recorded from scan sampling. For home range use, I used all recorded GPS points for each group. For feeding activity, I included only GPS points where at least 25% of scans

were recorded as foraging/feeding. For feeding activity within different habitats, I segregated the previous data on feeding activity by urban/edge and forest habitats on a map overlay. For each analysis, I used the formula:

$$I_d = n\left(\frac{\Sigma X^2 - N}{N(N-1)}\right)$$

where n is the total number of grid squares; X the number of points in each grid square; ΣX^2 the sum of values of X^2; and N the total number of points in all grid squares. The index is equal to 1 for a random distribution, less than 1 for a regular distribution and greater than 1 for an aggregated distribution. I computed overall indexes for each of the above factors for each group as well as monthly indexes.

For statistical analyses, I used monthly measures for each group, created by averaging diet, activity, habitat use and home range data over the three sampling days per month. Using the Kolmogorov–Smirnov test, I verified that all data were normally distributed and then used paired t-tests to compare monthly values for the two groups with respect to activity, diet composition and diversity, use of urban/edge and forest habitats, home range size, day range distance. Using Morisita's index of dispersion, I also used t-tests to compare the groups in terms of the spatial dispersion of home range use, feeding activity overall, and feeding activity within urban/edge habitats, and within forest habitats. I used SPSS 20.0 (SPSS, Inc., Chicago, IL) to conduct statistical tests with statistical significance (2-tailed) set at $P < 0.05$.

4. Results

4-1 Habitat resources

The two groups' home ranges differed in the availability of natural foods (Table 6). The monthly density of trees producing fruits, flowers and young leaves was lower for the "high anthropogenic" group (paired t-test: fruits, t = 1.85; df = 11; P = 0.045; flowers, t = 1.96; df = 11; P = 0.038; young leaves t = 3.23; df = 11; P = 0.004). The total number of plant species within the home range of the "high anthropogenic" group and plant species diversity (154; H = 4.022) were higher compared to the "low anthropogenic" group's (106; H = 3.539).

The number of refuse depository sites with exposed refuse was higher within the "high anthropogenic" group's home range (1.55 ± SEM 0.08, N = 36 sites per day) for the "low anthropogenic" group (0.85 ± SEM 0.05, N = 36 sites per day). Types of food available at refuse depositories included mostly cooked food like fast food, rice, noodles, fish, and meat. There was less exposed food available in the "low anthropogenic" group's home range because the two main refuse bins were constructed to be macaque-proof; however, items were at times discarded beside rather than inside the bins. For the "high anthropogenic" group, only one refuse bin out of the four depository sites was macaque-proof and other bins were readily accessible, with no deterrence except humans occasionally chasing the macaques away.

There was more visitor and car traffic for the "high anthropogenic" group (126.7 ± SEM 2.1 humans and cars per day) than for the "low anthropogenic" group (94.3 ± SEM 2.4 humans and cars per day), with most of the difference accounted for by traffic at the golf facility, which was within the home range of the "high anthropogenic" group. For both groups, traffic peaked in the early mornings, mid afternoons, and evenings. The early morning and evening crowds were mainly

joggers and people who visited the park to exercise. The mid-afternoon crowd consisted of people who visited the park to have their packed lunch or to rest. Some park visitors threw food to the macaques, which included left-over packed food, cultivated fruits (apples, oranges, and mangoes), peanuts, crackers, and bread.

4-2 Diet composition

As expected, the "high anthropogenic" group spent more time feeding on anthropogenic foods than the "low anthropogenic" group (Table 6, Figure 10; paired t-test: t = 3.656; df = 11; P = 0.004) and less time feeding on fruit (paired t-test: t = 10.315; df = 11; P < 0.001) and flowers (paired t-test: t = 5.198; df = 11; P = 0.002). There were no significant differences in time spent feeding on vegetative parts (young leaves, shoots, stems; paired t-test: t = 0.343; df = 11; P = 0.738). The "high anthropogenic" group fed on more species of food plants (36) compared to the "low anthropogenic" group (33; Table 7). Over the entire study period, the diversity of plant species consumed was lower for the "low anthropogenic" (H = 2.76) group compared to the "high anthropogenic" group (H = 2.94) but there were no significant differences in monthly diversity (paired t-test: t = 1.99; df = 11; P = 0.072).

4-3 Activity budget

Compared to the "low anthropogenic" group, the "high anthropogenic" group spent significantly less time resting (paired t-test: t = 4.20; df = 11; P = 0.001) and more time locomoting (paired t-test: t = 2.248; df = 11; P = 0.046; Table 6 and Figure 11). Time spent foraging/feeding was not significantly different between groups (paired t-test: t = 1.242; df = 11; P = 0.240).

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4-4 Habitat use

The "high-anthropogenic" group used significantly less forest habitat compared to the "low-anthropogenic" group (paired t-test: t = 4.864; df = 11; $P < 0.001$) but use of urban/edge habitats did not differ between groups (paired t-test: t = 0.478; df = 11; $P = 0.642$; Table 6 and Figure 12). Each group used both habitat types on all observation days. The "high anthropogenic" group showed higher feeding activity in forest compared to urban habitats (paired t-test: t = 2.30; df = 11; $P = 0.021$) but for the "low anthropogenic" group, there were no significant differences in feeding activity between forest compared to urban habitats (paired t-test: t = 1.48; df = 11; $P = 0.083$).

4-5 Ranging

The total home range, mean monthly home range, and daily ranging distance for the two macaque groups is given in Table 6. Mean monthly home range, whether overall or per day, was significantly higher for the "high anthropogenic" group compared to the "low anthropogenic" group (paired t-test: t = 4.44; df = 11; $P < 0.001$). The mean daily travel distance for the two groups did not differ significantly (paired t-test: t = 1.52; df = 11; $P = 0.078$).

4-6 Distribution of feeding activity and home range use

I compared the spatial distribution of feeding activity and home range use for the two study groups (Table 8). Compared to the "low anthropogenic" group, the "high anthropogenic" group showed significantly more spatial dispersion in overall

feeding activity, feeding activity in urban/edge and forest habitats, overall home range use and home range use in forest. I did not find significant differences in spatial distribution of general occupancy of urban/edge habitats.

5. Discussion

Although my study groups had partially overlapping home ranges, they showed clear differences in the amount of feeding on anthropogenic food resources and concomitant differences in feeding behavior, activity, and diet. The group that fed more on anthropogenic foods spent less time feeding on natural fruits and flowers. These differences could relate to the higher availability of anthropogenic resources; and lower availability of natural resources in the home range of the "high anthropogenic" group.

Most studies of food-enhanced primates report that food enhancement reduces home range size and day ranges, and causes animals to spend less time traveling and feeding, and more time resting (Chapter I). Such effects reflect the higher nutritional content and accessibility of anthropogenic food resources which reduced foraging cost. My results, however, contrasted with these patterns. Differences in activity budget and home range use between the two groups did not match contemporary predictions associated with these dietary differences. The "high anthropogenic" group spent less time resting and more time moving. This group also had a larger total home range and mean monthly home range compared to the "low anthropogenic" group. This difference could reflect the nature of food sources available to the macaques in this study and how they utilized them.

Anthropogenic food sources for primates include plantation crops, human habitation, waste depository sites, and direct human provisioning (e.g. Altmann & Muruthi, 1988; El Alami et al., 2012; Hockings et al., 2012; Riley et al., 2013; Saj et al., 1999; Strum, 2010). Similar to natural foods, these food resources may differ in availability and distribution; for example food sources like crops or waste depository sites are often spatially fixed and predictable, while direct human provisioning may occur at widely distributed sites and are less predictable both in space and time. In most studies of food-enhanced primates, food resources were abundant and concentrated (e.g. Altmann & Muruthi, 1988; El Alami et al., 2012) or were predictable (e.g. Altmann & Muruthi, 1988; Brennan et al., 1985; Fa, 1986). In such conditions, anthropogenic food exploitation could reduce foraging costs. The macaques in this study, however, derived anthropogenic food resources mainly from a few refuse sites, some of which offered limited quantities as they were designed to exclude macaques. Direct human provisioning was dispersed and irregular. Although there was some level of predictability in terms of the potential of obtaining anthropogenic food from these two sources during certain times of the day, when visitor traffic was high, actual quantities available could be highly variable. Macaques responded to traffic as if they associated it with provisioning, but not all visitors actually offered food. Refuse bins were also not filled on regular schedules with high quality food. The unpredictable availability of such foods meant that more effort to access provisioning and refuse sites, in particular, for the "high-anthropogenic" group, did not always necessarily yield much higher nutritional benefits. These conditions likely affected the macaques' foraging strategies and associated behavioral and ecological responses.

For example, I found that the "high anthropogenic" group showed significantly more dispersed overall feeding activity, feeding activity in urban/edge habitats and overall home range use. These results would not be expected if anthropogenic foods (which are generally higher in nutritional content) were abundant and/or clumped. A comparison between Barbary macaques which had access to fixed provisioning sites providing high quality food, and those which only had access to refuse sites, showed that macaques that fed on scarcer and more widely distributed refuse spent more time foraging and ranged further (Unwin & Smith, 2010). Similar effects have also been shown in rhesus macaques (Marriott, 1988). Macaques are primarily time minimizers that decrease their foraging effort by incorporating high return foods to meet their nutritional needs more easily but may utilize energy maximization when food availability is low (Menard & Vallet, 1997; Wrangham et al., 1998). The macaques in this study could exhibit a high degree of flexibility in utilizing these strategies.

Natural food resources could have also contributed to the higher activity and larger home range observed for the "high anthropogenic" group. For example, the lower absolute availability of natural food resources and more diverse overall natural diet composition for the "high anthropogenic" group could have led them to occupy and feed in forest habitat in a more dispersed fashion. Despite such adjustment, mean monthly dietary diversity did not differ significantly between the two groups and total dietary diversity was in fact slightly higher for the "high anthropogenic" group.

Thus, despite higher anthropogenic food resource exploitation, the "high anthropogenic" group still retained foraging characteristics comparable to conspecifics with a more natural diet, as researchers have found for other primate

species (e.g. De Freitas et al., 2008; McKinney, 2011; Naughton-Treves et al., 1998; Schurr et al., 2012).

The variable responses I observed in two groups of macaques with differential anthropogenic food resource utilization highlight the complexity of primate adaptive variability. Current knowledge on this subject derives mainly from comparisons between truly wild and highly food-enhanced primates, an approach that may be insufficient to understand the full repertoire of plasticity in primates, particularly at sites where they are highly commensal but nonetheless face various challenges in accessing anthropogenic food. Primates may be implementing adaptive foraging strategies in an environment that includes both natural and anthropogenic foods, a possibility that merits further detailed study.

Results like mine also highlight the importance of understanding within-population variation in the context of long-term population management. The Singapore macaque population exhibits various conflicts with humans that are caused mainly by macaque foraging behavior in urban habitats. If the behavior and ecology of different macaque groups at the same site varies according to how they differentially utilize food resources, then food resource related management tools like food exclusion, food supplementation, and diversion measures applied at a higher spatial or population level may achieve highly inconsistent results, intensifying the challenges for wildlife managers to ameliorate human-macaque conflict situations.

Chapter V

Temporal food resource correlates to the behavior and ecology of food-enhanced long-tailed macaques (*Macaca fascicularis*)

1. Abstract

I studied two groups of food-enhanced long-tailed macaques (*Macaca fascicularis*) that derived a quarter and half of their respective diets from anthropogenic food resources through human provisioning and feeding at refuse sites. The macaques alternated between feeding on natural food in the forest and feeding on anthropogenic food in adjacent urban areas. I found that dietary compositions of the macaques were correlated to natural fruit availability and macaques fed on natural fruits when available; but activity, habitat use and ranging patterns were correlated more to food availability from refuse sites and provisioning. Higher feeding on anthropogenic food resources was not correlated to natural fruit resource scarcity. Natural fruits constituted a highly variable resource base over the year and anthropogenic food resources provided a potentially more stable, albeit more opportunistic resource base. These results showed that the main drivers for macaque exploitation of anthropogenic foods were unlikely to be either natural food resource scarcity or a high dependence on anthropogenic foods. Behaviors associated with macaque anthropogenic food resource exploitation amplifies opportunities for

undesirable interactions between macaques and humans. Addressing the accessibility of anthropogenic food resources to macaques through management intervention should be a priority for mitigating human-macaque conflict issues in Singapore.

2. Introduction

In most forest ecosystems, there are marked fluctuations in food resource availability, with contrasting periods of relative resource abundance and scarcity (Leighton & Leighton, 1983; Raemakers et al., 1980). Variations in food availability, which may or may not be seasonal, affect the behavior, physiology and reproduction of many mammals (Lewis & Keppeler, 2005; Stephens & Krebs, 1987; Van Schaik et al., 1993). Adaptations to fluctuating conditions of resource availability are needed for mammals to survive in these environments, for example, seasonal breeding, use of habitat type and altitudinal range, shifts in diets, movement and activity patterns (Bodmer, 1990; Hanya et al., 2003; Hanya, 2004; Hemingway & Bynum, 2005; Leigh & Windsor, 1982; Leighton & Leighton, 1983; Tsuji et al., 2006; White, 1998).

In commensal long-tailed macaques, anthropogenic food resources may make up a significant proportion of total diet, with consequent impact on behavioral alteration (Chapter I). Long-tailed macaques in Singapore are found mainly along forest edges of the Central Catchment and Bukit Timah Nature Reserves, which are surrounded by urbanized areas (Chapter II). These macaques receive food directly from humans or forage on anthropogenic food sources like refuse bins, and are habituated and attentive to human food cues like plastic bags, as well as cars, because food provisioning frequently involves humans stopping their cars along

roads to throw food out of their car windows (Fuentes et al., 2008; Chapter III). At least 50% of the population obtained some of their diet from anthropogenic food sources (Chapter II). The interface between macaques and humans has led to conflict issues over space and resources (Chapter III).

In a previous study on the Singapore long-tailed macaques (Chapter IV), it was found that two neighboring groups of long-tailed macaques, a "high anthropogenic" group which fed on more anthropogenic food resources (49%) and a "low anthropogenic" group which fed on less anthropogenic food resources (26%) showed differential utilization of anthropogenic food resources, resulting in within-population variations in their behavior and ecology. The group that consumed more anthropogenic food spent less time feeding on wild fruits and flowers, less time resting, and more time traveling. They used forest habitats less often, and had a larger total home range and mean monthly home range. These results differed from what could be predicted by typical food-enhancement, which generally showed that food-enhancement resulted in smaller home ranges, shorter daily ranges, less time traveling and feeding, and more time resting. These confounding results were attributed to anthropogenic foods being derived mainly from a few refuse sites where they had limited access, and from dispersed and irregular human provisioning, compared to other studies where anthropogenic foods were largely spatially concentrated and abundant. The group that consumed more anthropogenic food therefore showed more spatially dispersed feeding activity and home range use. These results supported that considerable variations in diets exists within primate species and dietary flexibility can blur traditional assessments of expected behavioral characters like activity and ranging patterns (Chapman et al., 2002). The added

influence of anthropogenic food on the foraging ecology of commensal primates may thus be difficult to reliably predict through direct comparative approaches.

In this study, I examined the same groups of long-tailed macaques in Chapter IV to attempt at clarifying how different aspects of long-tailed macaque diet, activity, habitat use and ranging patterns are correlated to the temporal availability of natural and anthropogenic resources. I hypothesize that diet composition, activity, habitat use and ranging of the "low anthropogenic" group should correlate positively to temporal natural food availability and for the "high anthropogenic" group, to temporal anthropogenic food availability. These predictions should be expected since primate foraging, and associated behavioral characters are primarily determined by the spatial and temporal distribution of food resources that primates feed on, and the associated costs of obtaining these resources (Lambert, 2010; Oates, 1987). Elucidating how macaques respond to temporal variations in a anthropogenic habitat where both natural and anthropogenic food resources are utilized is important in improving an understanding of the foraging adaptations of human-commensal primates and the management of conflict issues.

3. Methods

3-1 Study area

This study was conducted at the Upper Seletar Reservoir Park on mainland Singapore (Figure 13). The park's borders include the Upper Seletar Reservoir, a divided highway, a golf course, a driving range and a military firing range. Golfers, anglers, joggers and school groups regularly visit the park for their respective recreation activities.

Two groups of long-tailed macaques are found in the vicinity of the Upper Seletar Reservoir Park (Chapter II; III; IV). They were observed to utilize urban park areas, as well as adjacent forested areas that are part of the nature reserves. The natural vegetation within the study area consisted of a matrix of young and mature secondary forests and freshwater swamp forests. Along the edge of the forest reserves and buffering the road and urban park areas are manicured grass patches, with native and non-native trees planted at regular intervals for shade and aesthetic effect.

3-2 Data collection

I collected data on diet, activity, habitat use and ranging of two groups of long-tailed macaques each month over a one-year period (June 2011 to May 2012). The groups were similar in size, with a range of 19 to 25 individuals in the "low anthropogenic" group and 21 to 30 individuals in the "high anthropogenic" group. I observed each group for three randomly chosen full days per month. I observed the "low anthropogenic" group in the first half of the month and the "high anthropogenic" group in the second half of the month. JS and an assistant located a macaque group at their sleeping site at dawn on each observation day and followed the group till dusk. JS recorded all relevant data while the assistant kept track of the movements of the macaques, recorded location data and marked feeding trees for identification. I logged a total of 398 hours of observation (mean ± SD: 11.1 ± 2.2 hours per observation day and 31.6 ± 3.4 hours per month) on the "low anthropogenic" group and 410 hours (mean ± SD: 11.4 ± 1.9 hours per observation day and 34.2 ± 2.6 hours per month) on the "high anthropogenic" group.

I used scan sampling (Altmann, 1974) at 15 minute intervals to record diet, activity and habitat use of macaques that were within sight, up to a maximum of 5 minutes, and from a left to right or clockwise direction to avoid repeated sampling.

Activity – I recorded the macaque groups' activity, including the following categories: rest, locomotion and forage/feed. Rest was defined as any form of inactivity, with the animal in a stationary, sitting, standing or lying position, with or without eyes shut. Locomotion was defined as progressive movement from one location to another, not followed by foraging or feeding behavior within 3 sec. Forage/feed was defined as eating or manipulating food items.

Diet – I recorded the macaque groups' diet by dividing the activity category forage/feed into two sub-categories, feeding on natural food and feeding on anthropogenic food. Actual food items and fruit species eaten by the macaques were also recorded, when they could be identified.

Habitat use – I recorded use of urban/edge and forest habitats by defining urban/edge habitats as areas including roads, concrete buildings, grass patches and planted trees on these patches. Forest habitats included only forested areas with continuous tree canopies.

Home range and daily range - I recorded group location at 15 minute intervals using a Geographic Positioning System (Trimble™ Recon, Trimble Navigation Limited, USA). This data was used to estimate the macaques' daily home

range using Minimum Convex Polygons (MCP), fixed mean method using "Home Range Tools" for ArcGIS® Version 1.1 (Rodgers et al., 2007) and Geographic Information System (ESRI ArcGIS™ 8.3, Environmental Systems Research Institute, USA 2005).   I used 100% MCP to represent the home range and corrected for areas of obvious non-usage, for example large water bodies. I also used this data to measure daily travel distance by summing straight line distances between sequential GPS points.

Natural food resources – I used fruit availability to represent seasonal natural food resource availability as long-tailed macaques are omnivorous but predominantly frugivorous, approximately 67% of diet (NRC, 2003). Temporal availability of natural fruits was estimated using 36 phenology plots measuring 20m by 20m that were set up within the home ranges of the macaque groups. Within these plots, I tagged all trees with Diameter at Breast Height (DBH) > 5 cm and monitored phenology of trees once each month. I followed methods by Chapman (1988) and Wich et al. (2006) which quantified fruit availability for primates by scoring the presence or absence of fruits.

Anthropogenic food resources – I used anthropogenic food availability from refuse bins and direct provisioning to represent seasonal availability of anthropogenic food resources. For refuse bins, I checked refuse sites found within the home ranges of the macaque groups once in the mornings before commencing group follows, and once at noon and scored the number of refuse sites with absence or presence of exposed refuse. Refuse sites were areas where refuse bins were

located, including large wheelie bins (660 litres), small plastic bins (60 liters) and fixed metal bins (100 liters). There was less exposed food available at the fixed metal bins, as they were constructed to be macaque-proof; however, items were at times discarded beside rather than inside the bins. Exposed refuse included any refuse items that were not contained and were retrievable by macaques, including styrofoam food boxes, plastic food packages and bits of food items in or around the refuse bins. Types of food available at refuse depositories included mostly cooked food like fast food, rice, noodles, fish, and meat.

To estimate food availability from provisioning, I used an indirect measure of human and car traffic. I conducted scans at one hour intervals at a predetermined point within each group's urban home range, to assess human and car traffic data, noting the number of humans and the number of cars. This data was collected independent of group follows. Visitors to the park directly provisioned the macaques by depositing food items at the side of the road or threw food to them while walking past or from their car windows. These were not always directly observable. As the macaques responded to traffic as if they associated it with provisioning; often approaching cars that stop by the roads (Fuentes et al. 2008; Chapter III), human and car traffic provided an inferential estimate of the potential of food provisioning. Items provisioned by humans included left-over packed food, cultivated fruits (apples, oranges and mangoes), peanuts, crackers, and bread.

3-3 Data analysis

For statistical analyses, data on diet, activity and habitat use were computed as mean percentages per month. Data on daily ranging distance and home range were

computed as mean distance in kilometer and kilometer square, per month, respectively. Fruit availability was computed as density of fruiting trees per month. I computed scores for refuse depository sites with exposed food, expressed as mean number of sites per day for any given month. I computed human and car traffic as total scores per day for any given month. All the above datasets consist of a total of 12 data points, each representing an individual month.

I used Spearman Correlation to examine the relationship, for individual groups across the year, between 1) proportion of feeding on anthropogenic food and fruits; and 2) mean daily ranging distance for each month and monthly home range. I used General Linear Model (GLM) to examine the proportion of variance explained by independent factors of natural food availability, represented by fruit availability; and anthropogenic resource availability, represented by refuse availability and human and car traffic. Diet, activity, habitat use and ranging data were considered separately as dependent factors in the GLM analyses. I examined the effect of temporal patterns of fruiting; human and car traffic and refuse availability separately for each group. I examined 1) proportion of time spent on a) fruit feeding and b) anthropogenic feeding; 2) proportion of time spent a) resting; b) locomoting; and c) feeding/foraging; 3) monthly home range area; and 4) daily ranging distance. All analyses were conducted using the Statistical Package for the Social Sciences version 20.0 (SPSS Ins., Chicago, IL). Statistical significance was set at $P < 0.05$. I calculated the Coefficient of Variation (CV) = Standard Deviation/Mean for a simple comparison of variability in natural food resource availability, refuse availability and traffic over time.

4. Results

4-1 Temporal resource availability

Within the "high anthropogenic" group's home range, fruit availability peaked from June to July, January to February and in May (more than 40 fruiting trees per hectare), and reached a low in October (less than 5 fruiting trees per hectare) (Figure 14a). The mean number of refuse depository sites with exposed refuse peaked in the month of September (~ 2 refuse sites per day) and reached lows in June and July (less than 1.5 sites per day) (Figure 14b).Visitor and car traffic peaked in the month of September (more than 125 humans and cars per day) and reached lows in May and July (less than 110 humans and cars per day) (Figure 14c).

Within the "low anthropogenic" group's home range, fruit availability peaked from May to June and February to March (more than 60 fruiting trees per hectare for these months) and reached a low in October (less than 10 fruiting trees per hectare) (Figure 15a). The number of refuse depository sites with exposed refuse peaked from November to December (more than 1 exposed refuse sites per day) and reached a low in August and April (~0.6 exposed refuse sites per day) (Figure 15b). Human and car traffic peaked in the months of June and December (more than 90 humans and cars per day) and reached a low in July (less than 80 humans and cars per day) (Figure 15c).

Over the year, variability in availability of fruit resources ("high anthropogenic" group – CV=0.62; "low anthropogenic" group – CV=0.60) was relatively higher than the variability in anthropogenic resources i.e. number of refuse depository sites with exposed refuse ("high anthropogenic" group - CV=0.18; "low

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anthropogenic" group - CV=0.21) and traffic ("high anthropogenic" group - CV=0.06; "low anthropogenic" group - CV=0.09).

4-2 Diet

For the "high anthropogenic" group, consumption of fruits over anthropogenic food was only higher for four months out of the year, in the months of March, May, June and July (Figure 16a). There was a significant negative correlation between consumption of anthropogenic food and fruits (r_s=-0.946; N=12; $P < 0.001$). For the "low anthropogenic" group, consumption of fruit accounted for the largest proportion of diet across all months of the year (Figure 16b). There was a significant negative correlation between consumption of anthropogenic food and fruits (r_s = -0.697; N = 12; P = 0.012).

I examined the effect of temporal fruiting availability, human and car traffic, and refuse availability on proportion of time spent on fruit feeding for both groups. For the "high anthropogenic" group, there was a significant positive relationship between fruit availability and the proportion of fruit feeding, with the overall model accounting for 63.6% of variance (Table 9a); and similarly for the "low anthropogenic" group, with the overall model accounting for 65.5% of variance (Table 9b). There were no independent factors contributing significantly to the models for both groups when I examined the effect of temporal fruiting availability, human and car traffic and refuse availability on proportion of time spent on anthropogenic feeding.

4-3 Activity

The proportion of feeding/foraging and locomotion activity was consistently higher than resting activity for the "high anthropogenic" groups across months (Figure 17a) but for the "low anthropogenic" group, only feeding/foraging activity was consistently higher than resting activity across months (Figure 17b).

I examined the effect of temporal fruiting availability; human and car traffic and refuse availability on resting activity. For the "high anthropogenic" group, there were no independent factors contributing significantly to the model. There was a significant negative relationship between fruit availability and traffic for the "low anthropogenic" group, with the overall model accounting for 80.2% of variance (Table 10a). I examined the effect of temporal fruiting availability; human and car traffic and refuse availability on locomotion activity. For the "high anthropogenic" group, there was a significant positive relationship between traffic and locomotion activity, with the overall model accounting for 62.0% of variance (Table 10b). For the "low anthropogenic" group, there were no independent factors contributing significantly to the model. I examined the effect of temporal fruiting availability; human and car traffic and refuse availability on feeding activity. There were no independent factors contributing significantly to feeding activity for both groups.

4-4 Habitat use

The proportion use of habitats showed some variations across months for both groups (Figure 18a and b). For the "high anthropogenic" group, the use of forest habitats was only higher than urban or edge habitats for six months of the year but for the "low anthropogenic" group, the use of forest habitats was consistently higher than use of urban or edge habitats throughout the year, except for Sep, Nov and Dec.

I examined the effect of temporal fruiting availability; human and car traffic and refuse availability on habitat use. For both groups, there were significant positive relationships between refuse availability and use of urban habitat. The overall models accounted for 75.8% of variance in habitat use in the "high anthropogenic" group and 87.8% in the "low anthropogenic" group respectively (Table 11a and b).

4-5 Ranging

Daily ranging distance for the "high anthropogenic" group ranged from 1.35 to 2.81 km per month and home range ranged from 0.039 to 0.115 km^2 per month (Figure 19a). There were no significant correlations between daily ranging distance and monthly home range (r_s = -0.112; N = 12; P = 0.729). Daily ranging distance for the "low anthropogenic" group ranged from 1.11 to 1.94 km per month and home range ranged from 0.011 to 0.036 km^2 per month (Figure 19b). There were no significant correlations between daily ranging distance and monthly home range (r_s = 0.537; N = 12; P = 0.072).

I examined the effect of temporal fruiting availability; human and car traffic and refuse availability on daily ranging distance. For the "high anthropogenic" group, there was a significant negative relationship between refuse availability and daily ranging distances, in an overall model that accounted for 52.3% of variance (Table 11a). For the "low anthropogenic" group, there was a significant positive relationship between traffic and daily ranging distances, in an overall model that accounted for 68.1% of variance (Table 11b). I examined the effect of temporal fruiting availability; human and car traffic and refuse availability on home range.   There

were no independent factors contributing significantly to home range for both groups.

5.   Discussion

5-1 Influence of fruiting seasonality and anthropogenic resources on diet

I found that despite differential anthropogenic food utilization, the diet composition of both macaque groups showed temporal correlations to natural fruit availability rather than to anthropogenic food availability. This was unexpected for the "high-anthropogenic" group which derived half its diet from anthropogenic food resources. This finding is important in filling a poignant knowledge gap to better understand the proximate causes for macaque exploitation of anthropogenic food sources, and resultant human-macaque interface.

Strategies employed by primates to exploit human food sources can develop in situations where natural resources may be insufficient for a population (e.g. Else, 1991), but more often simply because the animals have developed a preference for human food (e.g. Altmann & Muruthi, 1988; Forthman-Quick, 1986; Forthman-Quick & Demment, 1988; Malik & Southwick, 1988). Exploitation of different anthropogenic foods as fallback food in times of natural food scarcity and preferred foods even in times of high natural food availability, according to the nutritional value they provide, has also been shown in crop-raiding chimpanzees (Hockings et al., 2009).

In Singapore, there has been anecdotal (M. Shunari pers comm.) and empirical evidence (Lucas & Corlett, 1991) that during fruiting seasons, macaques had a lower

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reliance on anthropogenic foods. This implies that anthropogenic foods are supplementary to the macaque's natural diet, which may or may not be related to seasonal scarcity of natural fruit resources. However, historical and on-going anthropogenic food resource provisioning is also believed by many independent observers to have resulted in wild macaques developing a dependence on high energy foods and consequently, they do not optimally utilize natural food resources.

My results showed that the macaques in this study fed on natural fruits when temporally available. Natural fruits constituted a highly variable resource base over the year and anthropogenic food resources provided a potentially more stable, albeit more opportunistic resource base. Strong negative correlations were found between anthropogenic feeding and fruit feeding, indicating flexibility in the macaques' diet to balance the exploitation of either resource to satisfy their dietary needs. I did not find evidence of higher anthropogenic feeding in times of natural fruit resource scarcity, which has been shown in other studies, for example, Tibetan macaques (*Macaca thibetana*) (Zhao et al. 1991), capuchin monkeys (*Cebus apella*) (Siemers, 2000), Japanese macaques (*Macaca fuscata*) (Yamada & Muroyama, 2010) and long-tailed macaques (Lucas & Corlett, 1991). A previous study on the distribution and density of Singapore long-tailed macaques (Chapter II) inferred that it was unlikely that the carrying capacity of the macaque population exceeded the existing forest carrying capacity. These results showed that the main drivers for macaques to exploit anthropogenic foods were unlikely to be either natural resource scarcity or a high dependence on anthropogenic foods.

5-2 Influence of anthropogenic resources on activity, habitat use and ranging

In spite of the stronger influence of natural food availability on dietary composition, anthropogenic food resources played a considerable role in influencing several aspects of the macaque's activity, habitat use and ranging patterns. This was unexpected for the "low anthropogenic" group which derived only a quarter of their diet from anthropogenic food resources. I found that higher refuse availability correlated to more urban habitat use for both groups. I also found that higher human and car traffic used as an indirect measure of provisioning, correlated to higher locomotion activity for the "high anthropogenic" group and lower resting and longer daily ranging distance for the "low anthropogenic" group.

Anthropogenic food resources from refuse sites constitute a fixed locality resource and when these resources were abundant, the macaques expectedly spent more time foraging on these resources in urban habitats. For the "high anthropogenic" group, higher refuse availability also correlated to shorter daily ranging distances. This was also not unexpected as this group exploited more anthropogenic food resources as part of their diet, and when these foods were abundant, they did not need to travel long distances to forage for food.

The macaques in this study associated humans and cars with food provisioning (Fuentes et al., 2008; Chapter III). The positive relationship found between locomotion activity and traffic for the "high anthropogenic" group's could reflect a strategy to exploit the higher density of humans and cars by slowing down their ranging speed, with the expectation of food provisioning, without increasing their overall ranging distance. Locomotion activity was also higher than resting activity across all months for this group, indicating that they spent substantially more efforts foraging. Similarly, the negative relationship found between resting activity and

traffic; and positive relationship between ranging distance and traffic for the "low anthropogenic" group could reflect a similar strategy to exploit potential food supply from human provisioning. However due to lower overall traffic within their home range, exploitation of this food source could entail longer ranging but because they exploited this resource less often, locomotion activity did not consistently exceed resting activity across months. As lower resting activity for this group was also correlated to lower fruit availability, when conditions of both low fruit availability and high traffic occurred, the macaques could substantially increase their foraging effort to exploit human provisioning. The absence of expected correlations between longer daily ranging distance and larger home range could also be the result of strategies to exploit human provisioning by ranging in limited urban habitat areas.

Increased efforts by the macaques to obtain anthropogenic food did not however always translate into actual intake. Anthropogenic food resources in this study were spatially dispersed and unpredictable (Chapter IV). Provisioning occurred along several locations within the macaques' urban home ranges and not all humans and cars that interface with the macaques actually provided food. The quality and quantity of food found at refuse sites may also be highly variable. Despite this, anthropogenic food can provide advantages over natural food, for example, high simple sugar content, sweetness and low seed-to-pulp ratio in cultivated fruits compared to wild fruits (Milton, 1999), or different nutritional values like high carbohydrate content in rice (Hockings et al., 2009). The potential of obtaining these resources could have highly influenced their foraging strategies.

5-3 Opportunistic foraging adaptations accentuated by use of natural and anthropogenic resources

The macaques' persistence in areas that included both natural and anthropogenic habitats accentuated their opportunistic foraging adaptations. While dietary composition was mainly influenced by natural fruit availability, opportunistic exploitation of anthropogenic food is reflected in the macaques' persistence in edge habitats, which allowed them to seamlessly interface between fruit feeding in the forest and anthropogenic food feeding in adjacent urban areas, depending on resource availability. This could explain why overall dietary composition was correlated more to fruit availability, while other aspects of their behavior and ecology were influenced more by anthropogenic food availability.

Such adaptations could have blurred otherwise expected responses to food availability, either natural or anthropogenic. For example, I was not able to find resource predictors for several factors, including feeding activity, as well as home range size. The macaques' behavioral responses could be shaped by either or both natural and anthropogenic food resource factors considered in this study, making it difficult to elucidate clear resource correlates unless the effects were considerable. For example, smaller daily range area could be influenced by a combination of any of the following: higher fixed resource availability at refuse sites, more provisioning of high quality foods by one or few visitors, or higher natural food availability contributed by fruiting of spatially clumped or high productivity trees. Alternatively, these results could also indicate a degree of stability in certain aspects of the overall pattern of long-tailed macaque feeding ecology that is independent of temporal food resource fluctuation and distribution, as shown by Sussman (1987), and other primate species (reviewed by Garber, 1993). Primates that include both natural and

anthropogenic foods in their diet clearly add a complex dimension to considerations of mammal foraging adaptations and require more detailed examinations.

5-4 Implications for mitigation of human-macaque conflict

Various interventions have been implemented to mitigate human-macaque conflict throughout their range, often with mixed successes (Jones-Engel et al., 2011; Priston & McLennan, 2013). Mitigation measures targeted at reducing human-macaque interface through the manipulation of available food resources have almost always been undertaken in two complementary yet divergent approaches. One approach is based on diversion by increasing food resources through food supplementation, for example, controlled provisioning, or planting of food trees to draw macaques away from conflict areas (e.g. Huffman, 1991; Matheson et al., 2006; Shek, 2011). An alternative approach is based on exclusion through the reduction of anthropogenic food availability from human provisioning, access to refuse sites or crops (e.g. Cortes & Shaw, 2006; Honda et al., 2009).

Although both approaches involve reducing the potential for macaques to interface with humans through influencing macaque food resources, the underlying assumptions of their feeding ecology differ. Food supplementation measures are based mainly on the premise that natural food resources are insufficient to support existing macaque populations, thus requiring supplementation to reduce their potential to exploit anthropogenic food; while food exclusion measures generally assume that anthropogenic resources do not constitute a vital component of the macaques' diet, excluding which they could easily revert to natural food exploitation to satisfy their nutritional requirements.

The activity and ranging patterns of macaques in this study were largely influenced by anthropogenic food resource factors, but their diets were not highly dependent on these resources. These findings provide wildlife managers the opportunity to consider the rehabilitation of macaques back to their natural diets, in tandem with an anthropogenic food exclusion based approach; as restriction of anthropogenic food resources from refuse sites and human provisioning could likely resolve the bulk of problems associated with human-macaque interface. A case in example was shown by Kaplan et al. (2011) where an introduced artificial food patch into natural land within the home range of a baboon troop failed to significantly reduce their use of urban space; but the addition of access restriction to these waste sites using wire-mesh fencing resulted in a significant reduction in their use of urban space. Conflicts between humans and many mammal species present pressing challenges for wildlife managers. More consideration of the ecological responses of human-commensal mammals in anthropogenic influenced habitats is needed to determine effective approaches to management.

Chapter VI

General Discussion

1. Factors influencing human-macaque interface in Singapore

This study examined various aspects of long-tailed macaque ecology in Singapore in relation to human-macaque interface and anthropogenic food utilization. From results of the preceding chapters, I identified the key factors influencing human-macaque interface in Singapore.

The small total land area of the island state of the Republic of Singapore, coupled with a dense and growing human population is the overarching feature for inevitable increase in competition for space and resources between humans and wildlife. Singapore is now ranked third highest in population density in the world (CIA, 2012), with a projection to increase the population to 6.9 million by 2030 (NTPD, 2013); with complementary land use plans to support the projected population through major infrastructure development (MND, 2013).

Land conversion for development had already resulted in massive loss of natural habitats and consequent declines in biodiversity in Singapore (Chapter I). Against this backdrop of the development versus natural habitat protection conundrum, macaque populations have persisted. Populations of macaques are however living in increasingly close proximity to human habitation and activities (Chapter II) which appears to be the main driving factor for increasing

human-macaque conflict in Singapore. This was due partly to spatial patterns of land use, with roads and expressways that completely encircle the core macaque population located in the nature reserves; which is pressured by further development adjacent to their current range; as well as satellite populations embedded within human environments in fragments that are forced to interface with humans. These reserves are now forest islands, encircled by roads and expressways, with no buffer zones between the forest patches and human settlement. For example, at Bukit Timah, there are seven condominiums and one private estate located within 200m of the reserve, comprising around 1500 dwellings with approximately 6000 residents (Lee personal communication; Ooi et al., 2007). Some of these apartment complexes are less than five meters from the forest reserve border. This lack of buffer between urban Singapore and its forest reserves has resulted in an increased proximity between human and macaque populations, which creates a human-macaque interface zone where conflict between the two species can occur. This situation is further exacerbated by the natural riverine refuging behavior of long-tailed macaques, preferring forest edge and secondary habitat (Chapter I), with the modified landscape of Singapore providing an attractive niche on the edges of nature reserves and other forest fragments.

Macaque-human interface is encouraged by the availability of anthropogenic food resources in these habitats through human provisioning, exploitation of refuse sites and raiding of planted fruit trees and other food resources in and around residential areas. The macaques have learnt to associate humans with food and are habituated to human food cues like plastic bags, as well as cars, because food provisioning frequently involves humans stopping their cars along roads to throw

food out of their car windows. Human food provisioning has resulted in more than half of all of Singapore's macaques associating humans as a food source, and thus they are attracted to human activity (Chapter II). The role of human behavior in increasing human-macaque interface and conflict (Chapter III) is thus another key factor to consider. The motivation for provisioning macaques in Singapore is often directly linked to religious and/or cultural connections between humans and macaques, similar to other sites with Chinese and Hindu influences. People who provision macaques also regard the act as one of kindness or for pure enjoyment, but often with the perception that the macaques do not have enough food in their diminished forest habitats. There is however, a dichotomy between the two major groups interfacing with macaques - park visitors that only interact with macaques for short periods during their leisure time (and are more likely to provision macaques) and residents living near these areas that are likely to be more disturbed by macaques (Chapter III). This difference is because the costs associated with the human-macaque interface are greater for residents who must frequently interact with macaques during their daily lives; and are more likely to suffer loss or damage of property than visitors. Human-macaque conflict is thus indirectly related to a human to human conflict situation, where the actions of one group of people have undesirable implications for the other.

Direct human behavior towards macaques is also largely responsible for increased human-macaque interface (Chapter III). For example, human provocation of macaques accounted for one-quarter of all recorded macaque-human interactions. The majority of macaque-to-human interactions were also related to macaques locating and obtaining food but this was contributed by two-thirds of interactions

occurring when a human was carrying food or food cues. The rates of actual interactions between humans and macaques were however low compared to other countries with human-macaque interface and the severity of interactions is benign in terms of occurrences of injuries to humans from macaque bites or scratches. Despite this, perceptions of macaques are often misconstrued by erroneous interpretations of macaques being aggressive and this was exacerbated by biased press reports and media depictions of nuisance macaques generated from the complaints of a small proportion of affected people. The perceived severity of macaque conflict problems has contributed to an exaggerated interpretation of the actual situation of human-macaque interface in Singapore.

Anthropogenic spatial and behavioral factors have influenced the natural behavior and ecology of long-tailed macaques (Chapter IV and V), with within-population variability in diet, behavior, habitat use, and ranging patterns reflecting differential utilization of anthropogenic food resources. The effects of higher anthropogenic food resource utilization however, contrasted with previous studies of food-enhanced primates. This was due mainly to anthropogenic food resources being limited and dispersed compared to most interface sites where food resources were abundant and concentrated. Dietary compositions of the macaques were correlated to natural fruit availability and macaques fed on natural fruits when available; but activity, habitat use and ranging patterns were correlated more to food availability from refuse sites and provisioning. Higher feeding on anthropogenic food resources was also not correlated to natural fruit resource scarcity. These results showed that the main drivers for macaque exploitation of anthropogenic foods were unlikely to be either natural food resource scarcity or a high dependence on

anthropogenic foods, but more related to the habituation and opportunistic exploitation of such foods by macaques. Adapted behaviors associated with macaque anthropogenic food resource exploitation is thus a key factor in human-macaque interface that often escalates into conflicts.

In summary, this study identified several key factors that influenced human-macaque interface and conflicts in Singapore, namely, spatial land use and development patterns that resulted in increased proximity between humans and macaques; direct and indirect human behavior that resulted in habituation of macaques to anthropogenic foods and an escalation of an otherwise largely benign human-macaque interface situation. Findings from this study also debunked some misconceptions about the factors that influenced human-macaque conflict, namely, large macaque populations; lack of sufficient natural food resources; and a high dependence of macaques on anthropogenic foods as drivers for increased human-macaque interface and conflicts.

2. Comparison of the human-macaque conflict situations between Japan and Singapore

The association between Japanese and Japanese macaques spans a long history, dating back some 35,000 years (Mito & Sprague 2013). There has been historical conflict arising from the interface between macaques and humans in Japan, which has intensified since the 1970s, where crop damage by Japanese macaques became a significant issue of concern (Knight, 1999; Mito & Sprague, 2013). Similarities and differences between the human-macaque conflict situation in Japan and Singapore can be drawn from comparisons of the context of human-macaque interface.

Similar to Singapore, trends of increasing conflict throughout the later part of the 20th century and to present are evident in Japan (Ministry of Agriculture, Forestry and Fisheries 2009; Mochizuki & Murakami 2011). The overarching postulated cause of increased human-macaque conflict in Japan (Muroyama & Yamada 2010; Sprague 2002; Suzuki and Muroyama 2010) is similar to the conclusion for Singapore in my study i.e. owing to general encroachment of natural forests, resulting in closer proximity to areas of human activity. The underlying factors however differed. For example, one of the reasons for increasing conflict between Japanese macaques and Japanese was attributed rural depopulation of plantation areas, resulting in macaques having easier accessibility to crop areas; whereas the main factors in Singapore were infrastructure expansion along the edges of forest reserves and increasing human population interface. In addition, the impact of direct economic damage varied between the two contexts. In Japan, crop raiding by Japanese macaques cause significant monetary losses each year (Idani et al., 1995; Ministry of Agriculture, Forestry and Fisheries, 2009). As noted in Chapter II, crop-raiding by macaques is not relevant in the Singapore context, as there is no agricultural industry of note in Singapore. However, other forms of damage are similar, for example, damage to village houses, entering of houses and raid kitchens, taking food from village shops and tourist inns, and sometimes attacking children, housewives and elderly people carrying shopping (Knight, 1999).

Another significant difference lies in the context of voluntary interactions between humans and macaques. In Japan, monkey parks were set up in many areas to encourage interactions between humans and macaques through tourism; and for conflict management and conservation purposes (Mito, 1995). In these monkey parks,

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visitors are encouraged to interact with macaques by feeding them (Knight, 2005). In Singapore, macaque feeding is instead discouraged and even penalized in park and nature reserves (this chapter). Similar contexts of human food provisioning that is based on compassionate perceptions that the macaques do not have enough food in their natural habitats also occurs in Japan (Ochiai 1991).

Similar to Singapore, conflict issue between Japanese and Japanese macaque has similarly raised general public and media attention on a national level; with proponents both for and against the implementation of management measures like culling; and opinions based on differing economic, cultural and conservation perceptions (Watanabe, 1995). Compared to other areas with human-primate conflict, the Japanese generally have a higher tolerance to macaque problems, owing largely to the close historical association between the people and macaques (Hill & Webber, 2010).

2. Management of human-macaque conflict in Singapore

The main wildlife governing agencies for macaques, the Agri-Veterinary Authority of Singapore (AVA) and the National Parks Board Singapore (NParks) recognizes the human-macaque conflict issue as one which requires mitigation. Numerous initiatives were implemented to attempt at ameliorating these conflict issues.

NParks had attempted several strategies to curb the feeding of macaques. In Singapore, it is an offence punishable with fining to feed monkeys within the boundaries of the nature reserves since 1997, under the National Parks Board Act, Chapter 198A (NParks, 1997). The cost of fines had been increased over the years.

The penalty for persons caught feeding macaques was increased from SGD$200 to $250 in 2007 and in 2008, this was raised to SGD$500 (NParks, 2008). NParks had also used closed-circuit television cameras along feeding ''hotspots'' to observe feeding and has also worked cooperatively with auxillary police to assist in the issuance of feeding fines within park boundaries. Education programs were also conducted around nature reserve areas to alert people of the feeding ban through signage and directly informing residents and visitors by engaging them or issuing informative pamphlets. To further limit the availability of anthropogenic foods to macaques, exclusion devices like macaque-proof bins were also installed in all parks and nature reserves under NParks management. Official advisories were also regularly provided to residents living close to macaque populations, to advise them on how to minimize macaque nuisance problems; for example, simple food exclusion practices like closing of windows and doors in their homes or installing window mesh/grilles on windows and doors, proper disposal of refuse, and keeping visible food sources out of sight. Efforts have also been made to manage the Singapore macaque population, predominantly through trapping. Such efforts have shown an increasing trend over the past decade since 1996. Trial sterilization programmes were also conducted on two groups of macaques at Lower Peirce Reservoir Park in 2007. Other efforts included the translocation of macaques captured from problem areas into the CCNR in 2005.

Despite these efforts to ameliorate human-macaque conflict, complaints about macaque problems remained unabated and even showed increasing trends. In 2010, 1200 complaints were lodged to the management authorities, and this was almost double what was reported in 2008 (Feng, 2011); and more than double what

was reported in my study in 2007 (Chapter II). These trends suggest that the key factors influencing human-macaque interface may not been sufficiently addressed.

Management efforts by Singapore's wildlife management and land planning agencies are crucial in reducing human-macaque conflict through proper urban development plans aimed to minimize human-macaque overlap. Firstly, the development of areas adjacent to macaque habitats has continued in recent years with numerous new condominiums constructed right at the edge of forest reserves; hence increasing the overlapping zones between human habitation and macaque habitats (Chapter II). These developments are often marketed under the theme of "living close to nature" but unfortunately fail to anticipate potential problems associated with human-macaque interface. The issue of development is difficult to address due to intrinsic housing needs for an expanding population and commercial profitability, but can be mitigated through policy level regulations. This can be done through the implementation of buffer zones between development areas and forest habitats to provide protection to the reserves and their wildlife, as well as to shelter human settlement from Singapore's nature reserves. Design of buildings that help exclude macaques from entering the premises should be encouraged, for example, smooth and/or tall walls, etc and eliminating the potential for macaques to utilize overhanging tree branches as bridges to surmount these physical exclusion barriers. Potential occupants of these new developments should also be sufficiently educated and informed of the possibility of macaque nuisance during the sales process. These efforts can be built into the Corporate Social Responsibility facet of developers. Inclusion of clauses related to the expectation of nuisance problems for residents living near forest reserves can also be included into URA/SLA (Urban

Redevelopment Authority/Singapore Land Authority) purchase or rental contracts and more responsibility can be assigned to the URA to properly assess and mitigate developments near forested areas where monkey populations are present. In addition, many problems associated with macaque habituation to human food are initiated during the construction phase, where construction staff begins to feed macaques that range close to these areas or expose food resources through improper refuse disposal. Regulations to limit such possibilities can be implemented as best practices through the Urban Redevelopment Authority (URA) or Building and Construction Authority (BCA). A formal process of impact assessment prior to the start of a housing development would be instructive in avoiding areas of probable human-macaque conflict.

Secondly, the availability of anthropogenic resources for macaques to exploit needs to be further addressed. In Chapters IV and V, I showed that the availability of anthropogenic food was the main factor that influenced activity and ranging patterns associated with increased human-macaque interface. Exclusionary devices like monkey-proof bins have proved relatively successful in reducing potential food sources in reserve areas although implementation of such measures in adjacent areas that are not part of the nature reserves is dependent on the perusal of private owners. This was evident in this study at Upper Seletar Reservoir Park, where although macaque-proof refuse bins are put in place by NParks, macaques still had access to uncovered refuse bins within their home range, from food and beverage and retail operators in the vicinity. The issue of macaque food provisioning also needs to be better addressed. Lucas (1995) reported that notices erected to discourage people from feeding macaques in 1987 had no effect a year later and the situation appears

unchanged a decade later. This statement still holds true more than two decades on. In 2010, 300 people were fined for macaque feeding offences, twice that of previous years (Feng, 2011). It appears that alternative approaches may be required to augment the penal approach to macaque provisioning. Close attention also needs to be paid to the development of behavioral management and conservation communication programs to control human behavior in interface zones since it is known that feeding is a major attractant of macaques to human settlement, and often the initial trigger for conflict.

Thirdly, some existing management measures may have been implemented without sufficient consideration for the actual factors that influence human-macaque interface. For example, substantial effort is put into the trapping of macaques based on the justification that population size is directly correlated to nuisance problems. In Chapter II, I did not find empirical evidence of unusually large macaque populations or high densities in Singapore, compared to many other areas with human-macaque interface and even some wild populations. Related to this is the widely held notion that the carrying capacity of remaining Singapore forests is insufficient to support the existing macaque population, thus resulting in their reliance on anthropogenic foods. In Chapters I, IV and V I found that the macaques in Singapore naturally lived close to forest edges adjacent to human habitation, regardless of the availability of natural food resources; especially where anthropogenic food resources are available. They were also not highly dependent on anthropogenic food resources to satisfy their dietary needs. Reconsideration of mitigation measures emphasizing on anthropogenic food restriction, rather than macaque population management are required.

The conflict between long-tailed macaques and people in Singapore had been highlighted as an escalating issue by the media and management authorities in recent years. Singapore indeed suffers from problems associated with humans living in close proximity with macaques, but the results of this study indicated that Singapore may have one of the most benign human-macaque interfaces in the world (Chapter III); and there is ample public support to mitigate human-macaque conflict through a co-existence model. Human–wildlife conflicts are often manifestations of underlying human-human conflicts, such as between authorities and local people, or between people of different cultural backgrounds (Dickson 2009). A similar situation of conflict between visitors and residents were also shown in the Singapore context (Chapter III). Such evidence suggests that social factors, rather than actual wildlife damage can be more important in driving conflict (Dickson 2009). Addressing the socio-political facet to human-macaque conflict is critical to enabling such a resolution. Education and outreach efforts play an important role in shaping the perceptions and tolerance levels of the general public to macaque nuisance problems; but perhaps, more importantly, is the modification of the approaches of policy makers and management authorities to human-macaque conflict mitigation. The current conflict management paradigm is based largely on the view that macaques are an expendable pest species and that pest control measures are appropriate management measures. Such mentality directly translates into the choice of management actions. For example, a positive relationship was found between macaque trapping and the number of public complaints (Chapter II); and this showed that macaque removal efforts had largely been utilized as a response tool to appease public sentiment. The failure of such management efforts can however result in

deteriorating public sentiment and increasing frustration, putting more pressure on management authorities to be obliged to deliver reactive solutions just to appease complainants, instead of attempting at arriving at mutually beneficial solutions, where complainants are regarded as contributing stakeholders to the problem. Such management measures that are not based on adequate rationale also opens management agencies to attacks from animal welfare advocates.

The Republic of Singapore is renowned internationally for its strict governance and strong political will to affect changes at all levels of society through continuing social education and engineering of social behavior and attitudes through mass media, campaigns and legal binds (Savage & Kong, 1993). Coupled with the small size of the country and limited natural resources, it provides a unique setting for exploring an ideal management model for human-macaque conflict resolution in urban landscapes. Better long-term planning and application of management measures based on scientific rationale will bring us closer to an ideal management model for a sustainable macaque population in an urban landscape. An ultimate resolution to the human-macaque conflict situation in Singapore also depends largely on decisions at a policy level where current ambivalence by policy makers towards recognizing macaques as an important wildlife heritage needs to be reversed and cultivated throughout all ranks of society.

4. Limitations and Further Studies

The conclusions to various aspects of this study were limited by several factors that will be discussed in this section. Based on these limitations, further studies are recommended.

In Chapter II, I refrained from making actual predictions on population growth trends. The relationship between macaque population size and density and increasing human-macaque conflict was thus not conclusive. This limitation was due to difficulties in comparing different population estimates with possible differences in thoroughness, sampling effort (for example, actual areas surveyed) and methods used. The earliest source of population data was from the Malayan Nature Society survey in 1986 which estimated the long-tailed macaque population on mainland Singapore. Subsequent sources of available data i.e. Teo and Rajathurai (1997) and Agoramoorthy and Hsu (2006) only covered the NR areas and some discrepancy exists between these estimates when directly compared. However, some general inferences of macaque population growth rate could still be made by comparing available population estimates from these studies. Comparing the population size for Singapore of 1000 individuals estimated by Malayan Nature Society (1986) to the current estimate of 1454 individuals, it represented a compounded annual increase of 1.8% annually. Comparing Teo & Rajathurai (1997) which estimated 850 individuals within NR to 1027 individuals in this study, it represents a 1.9% compounded increase annually. Comparing Agoramoorthy & Hsu (2006) which estimated 635 individuals within the NR in 2004, it represented a compounded increase of 17.4% annually. This last comparison however appeared unrealistic as it would also entail a compounded population decrease of about 4.1% annually from 1997 to 2004, during which no major catastrophes or large-scaled culling of macaques occurred to suggest such a population decrease. Inferred population growth rates over the past two decades were thus likely around the region of less than 2% annually. The spike in conflict issues over the past decade may not be directly correlated to an intrinsic

increase in macaque population size, as inferred, but determined more by their distribution in forest edges near human activity. This however does not discount the possibility that an increase in macaque population, accumulated through compounded annual increments over many years (and beyond a certain threshold at a certain historic point of time) had triggered an initial increase in human-macaque interface and resultant conflict issues. Longer-term monitoring of macaque populations and population dynamics using methods that are directly comparable, are needed to arrive at more conclusive results. However, limited established sampling methods are available for surveying primates in semi-urban habitat conditions. Due to the small area and fragmented habitat conditions of Singapore's forest and large bias in distribution of macaques along forest edges, the use of sampling methods like line transects using distance sampling violates many of the key assumptions to justify its use. A more accurate method to monitor population growth rate was demonstrated by the on-going work led by M. Gumert which identified all individuals of several groups of macaques at Bukit Timah for long-term monitoring. Inferences made from a select population may however be limiting but implementing this method on a Singapore-wide scale would be unrealistic due to the effort involved. The monitoring of a reasonable sample of different macaque groups at different sites across Singapore may be a more realistic option.

Related to the above, my conclusion on higher long-tailed macaque densities along forest edges, compared to the forest interior; as well as the inference that the carrying capacity of the Singapore forests was unlikely to have been exceeded judging from density estimates, was based primarily on the finding that the distribution of macaques was mostly at the edges of the forest, and very few macaque

groups were found within the forest core. Consequently, it could also represent an underestimate of overall population size if indeed macaques occur in higher densities in interior forests than what I estimated. Although it was suggested in Chapter II that the large observed differences was unlikely to be due to bias in survey methodology which was based mainly on walking trails generally nearer to forests edge habitats, further confirmation is required.

My analysis on provisioning of long-tailed macaques in Chapter II was based on a rapid indirect method (i.e. plastic bags as cues and limited observation of anthropogenic resource exploitation) for estimating such trends within the Singapore population. Although a more detailed method (human and car traffic as indices of provisioning) was used for such analysis in Chapters IV and V, there are limitations to these methods due to the lack of directly quantifiable measures of actual provisioning. The constrains were due to difficulties in observing and recording independent events of human provisioning because 1) human provisioning occurred more frequently when the macaques were visible to provisioners in urban areas, thus creating a non-independent bias; and 2) manpower needed to record comprehensive provisioning events simultaneous with macaque group follows to record macaque behaviors and movements. A possible solution to this problem in future studies can include the use of GPS telemetry, trials of which have been successfully conducted by the University of Notre Dame team led by A. Fuentes; to free up observation effort for simultaneous provisioning events and exploitation of anthropogenic resources. The use of GPS telemetry technology can also provide larger samples of high resolution data for comprehensive analyses of ranging patterns in urban habitats, which is currently being conducted by A. Klegarth. My quantification of

anthropogenic food resources available to macaques (estimation of sites with exposed refuse) faced a similar limitation, as the actual quantity of food at each site was difficult to quantify using rapid methods of measurement. A potential solution is the use of stable isotopes $\delta^{13}C$ and $\delta^{15}N$ to estimate the levels of natural and anthropogenic diets instead of direct observation (e.g. Schurr et al. 2012; Schillaci et al. 2013).

My analysis on aspects of long-tailed macaque population dynamics like annual attrition rate was also limited by the availability of more comprehensive longitudinal information on parameters like road kills and natural mortality. Similar limitations were faced in the collation of more detailed information on trends of public complaints and trapping data. These information were separately obtained from management authorities like NParks and AVA and were largely dependent on individual staff effort to collate these data and making them available for use by researchers. A more unified and systematic commitment to long-term collation of such data, coupled with higher resolution in data collection, in terms of trapping locations and nature of public complaints (including profiles of complainants), etc is necessary to better assess long-term trends and correlations, as well as to monitor the success of implemented management measures.

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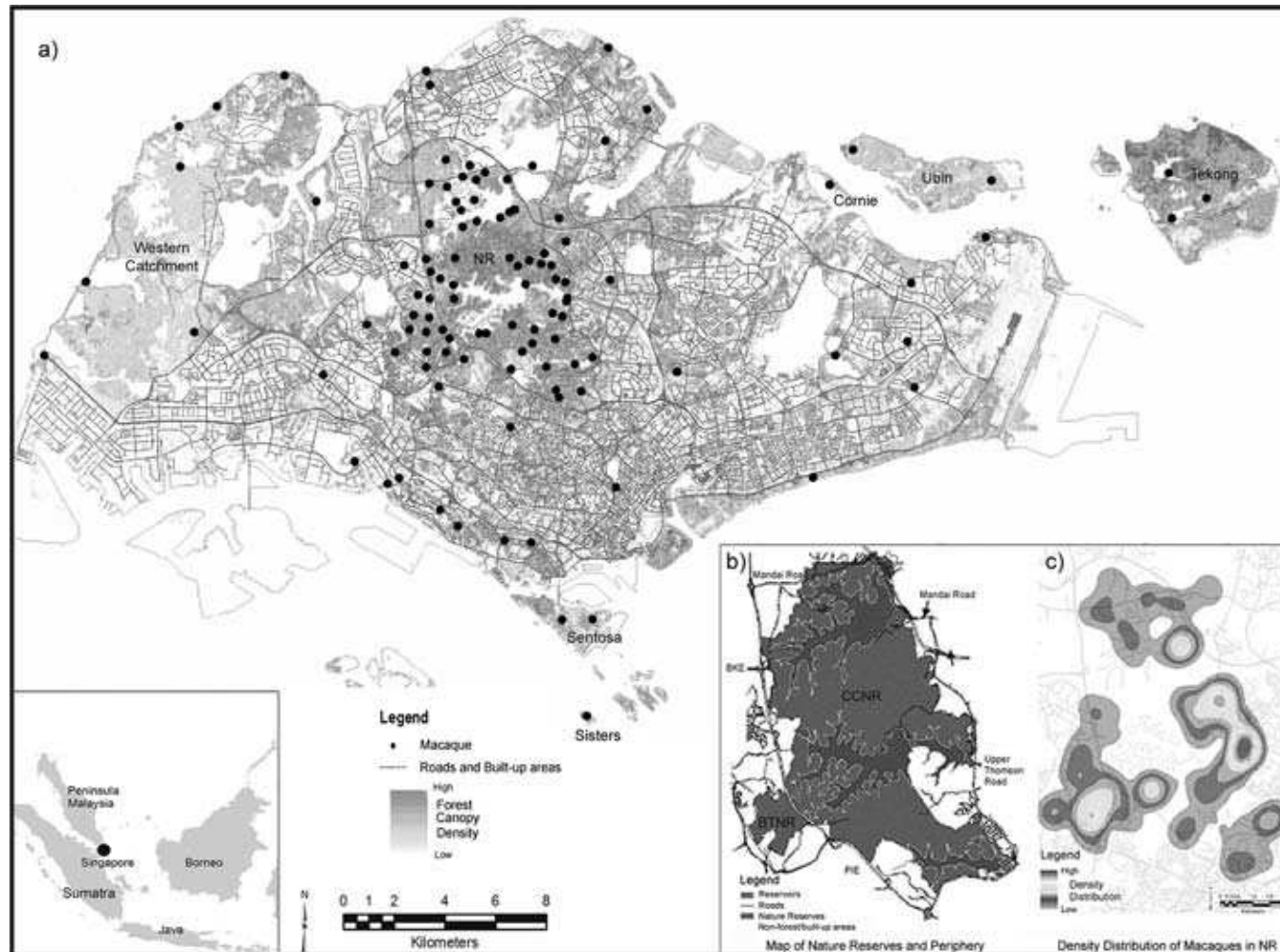
Figure 1: a) Distribution of macaque groups on forest cover b) map of Nature Reserves and periphery c) density distribution within NR
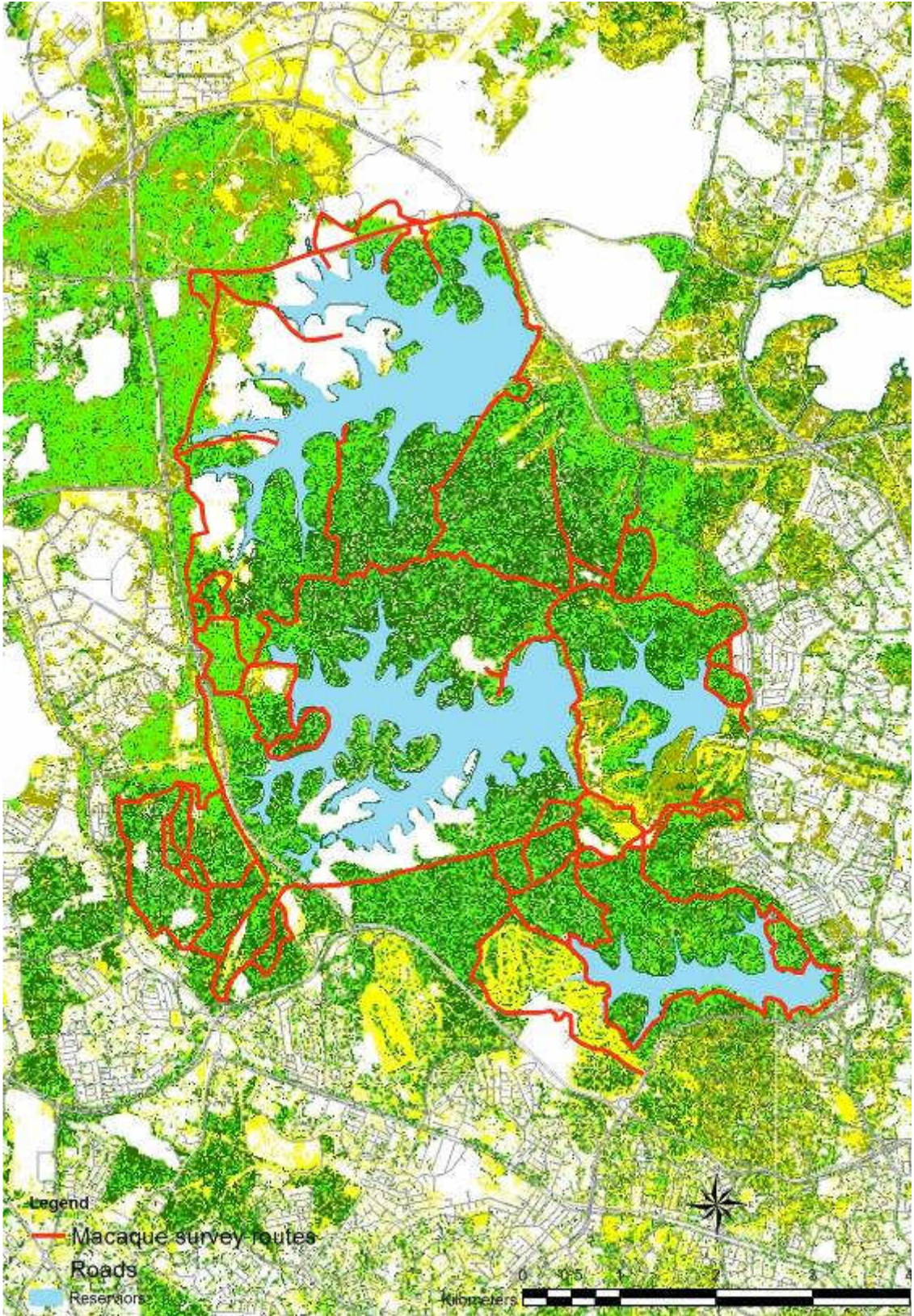
Figure 2: Survey routes within NR.

Table 1a: Locality, estimated group size and information source of macaque groups.

Reference	Locality	Est. Group Size	Source
Bukit Timah Zone	BTNR (Main road)	56	Survey
	BTNR (Senapang)	22	Survey
	BTNR (Summit)	10	Survey
	BTNR (Dairy farm)	22	Survey
	BTNR (Old nursery)	7	Survey
	BTNR (Asas)	8	Survey
	Belukar Track	8	Survey
	Rifle Range Road (Kg. Chantek)	16	Survey
	Rifle Range Road (Flyover)	18	Survey
	Jln. Anak Bukit	29	Survey
MacRitchie Zone	Rifle Range Road (CIS)	28	Survey
	Rifle Range Road (CIS)	23	Survey
	Sime Road (SICC)	25	Survey
	CCNR MacRitchie (golf link)	11	Survey
	CCNR MacRitchie (TTW)	14	Survey
	CCNR MacRitchie (Bukit Kalang)	27	Survey
	CCNR MacRitchie (Shinto)	5	Survey
	CCNR MacRitchie (MNT)	11	Survey
	CCNR (Venus link)	10	Survey
	Island Club Road (Island Location)	33	Survey
	CCNR MacRitchie (Petai Boardwalk)	17	Survey
	MacRitchie Reservoir Park	35	Survey
	CCNR MacRitchie (Lornie Trail)	13	Survey
Mandai Zone	CCNR (relocated from Zoo in 2005)	18	B. Martelli pers comm. (sighted Nov 2007)
	CCNR	8	B. Martelli pers comm. (sighted Nov 2007)
	CCNR	6	B. Martelli pers comm. (sighted Nov 2007)
	Chestnut Trail	10	Survey
	Chestnut Trail	10	Survey
	Mandai track 15	10	Survey

Table 1a. Continued

Reference	Locality	Est. Group Size	Source
Mandai Zone	Mandai track 15 (PUB)	10	Survey
	Temple Trail	5	Survey
	PUB station	8	Survey
Nee Soon and Lower Peirce Zone	Lower Peirce Reservoir Park	66	Survey
	Lower Peirce Reservoir Park	32	Survey
	Lower Peirce Reservoir Park	22	Survey
	Lower Peirce Resevoir Park	14	Survey
	Old Upper Thomson Road	45	Survey
	Old Upper Thomson Road	20	Survey
	Old Upper Thomson Road	18	Survey
	Old Upper Thomson Road	27	Survey
	Upper Peirce Reservoir Park	26	Survey
	Upper Peirce Reservoir Park	18	Survey
	Peirce Track	15	Survey
	Upper Seletar Reservoir (Roundabout)	22	Survey
	Upper Seletar Reservoir Park	30	Survey
	Upper Seletar Reservoir Park	19	Survey
Upper Seletar Zone	Mandai Lake Road (Mandai camp)	23	Survey
	Mandai Lake Road (Stephen Lee Woods)	15	Survey
	Zoo	10	L. Meijer; C. Yeong pers comm. (Sighted 2007)
	Night Safari	10	L. Meijer; C. Yeong pers comm. (Sighted 2007)
	Night Safari	10	L. Meijer; C. Yeong pers comm. (Sighted 2007)

Table 1a. Continued

Reference	Locality	Est. Group Size	Source
Upper Seletar Zone	Upper Seletar North	16	Survey
	Upper Seletar North	6	Survey
	Ulu Sembawang Forest (Upper Seletar)	6	Survey
	Mandai Columbarium	22	Survey
2	NTU/Longyao	11	Survey
3	Western Catchment (Poyan)	15	Survey
4	Western Catchment (Track 13)	25	Survey
5	Western catchment (Sarimbun)	2-3	S. Rajathurai pers obs. (sighted 2004/2005)
6	MOE Jln Batera Adventure Center	~5	Interview public (sighted Feb 2007)
7	Sg. Buloh	~5	Suparti pers obs. (sighted July 2007)
8	Lorong Kebasi	1 group	G6 Army pers comm. (sighted 2007)
9	Asrama	20	W. Ng pers comm. (sighted Oct 2006)
10	Ulu Sembawang Forest (Lada Hitam)	10+	S. Rajathurai pers obs. (sighted Mar 2007)
11	Woodlands	23	Survey
12	Marsiling	16	Survey
13	SAF Yacht Club	2-3	Interview public (sighted Mar 2007)
14	Sembawang Park (Bottle tree park)	3	Interview public (sighted Jan 2007)
15	Katib Bongsu	1 or more	W. Ng pers comm. (sighted June 2007); Robin Ngai pers comm.
16	Yishun Park	3	Survey
17	Sembawang Country Club	20+	Interview SCC staff (sighted 2007); T.L. Lim pers comm. (sighted Sep 2007)
18	Springleaf	8	Survey
19	Tagore	5-10	Interview public (sighted July 2007)
21	Cornie Island	3	Lahiru pers comm. (sighted 2006)
22	Pulau Ubin (Tg. Tajam)	2	S. Rajathurai pers comm. (sighted Jan 2005)

Table 1a. Continued

Reference	Locality	Est. Group Size	Source
23	Pulau Ubin (Kg. Melayu)	10-15	R. Teo pers comm. (sighted 2007)
24	Pulau Tekong (near reservoir)	3+	S. Rajathurai pers obs. (sighted 2003)
25	Pulau Tekong (Tekong highway, swimming pool area	33	Subaraj Rajathurai pers obs. (sighted Oct 2007)
26	Pulau Tekong (Grenade range)	22	S. Rajathurai pers obs. (sighted Dec 2002)
29	Tampines St. 22	2	Public complaint (July 2007)
30	Simei	3	Public complaint (July 2007)
31	Bedok Reservoir Park/Paya Lebar airbase	3-5	Public complaint (August 2007)/Airforce complaint (Sep 2007)
33	Toa Payoh/Braddell Road	4	The New Paper, 4 Jul 2007/Straits Times 29 Dec 2007
34	Mount Pleasant	16	Survey
35	Bukit Brown Cemetary	19	Survey
37	Botanic Gardens/Tyersall	1-3	S. Rajathurai pers obs.. (May be from MacRitchie/Bukit Brown area)
38	Chestnut Ave.	14	Survey
40	Bukit Panjang Park	2	Interview public (May 2008)
41	Bukit Batok Nature Park	32	Survey
42	British Club	8	Survey
43	Malayan Railway/Clementi	1-10	Interview staff (sighted May 2007); H. Samri pers comm.. (sighted Nov 2007)
44	Jurong East IMM	1 group	Sin Ming Daily News 24 May 2006
48	NUS Science Lab	3	R. Clements pers comm. (sighted Aug 2007)
49	Kent Ridge Park	1 or more	Public complaint (Oct 2006)
50	Mount Faber Park	4	A.Y. Tan (sighted Mar 2007)
51	Telok Blangah Park/Telok Blangah Road	1-3	Interview public (sighted early 2007); NParks staff pers comm. (sighted Nov 2007)/Sin Ming Daily News 22 Dec 2007
53	Sentosa Island	2	W. Ng pers comm. (sighted 2007) 34-42 between 2003-2004 (S. Rajathurai pers comm.)

Table 1a. Continued

Reference	Locality	Est. Group Size	Source
54	Sentosa Island (Mt. Serapong)	10	Subaraj Rajathurai pers obs.
55	Sisters Island	15	S. Rajathurai per sobs.; R. Teo pers comm. (sighted 2000) (SDC staff reported as large as 45-50, inclusive relocated monkeys from Sentosa)

Table 1b: Locality and information source of solitary male macaques.

Reference	Locality	Source
Nee Soon and Lower Peirce Zone	Old Upper Thomson Road	Survey
Upper Seletar Zone	Upper Seletar Reservoir Park	Survey
1	Western Catchment (Tengah area)	S. Rajathurai pers obs. (sighted 2004)
20	Ang Mo Kio Town Garden West/Ave 1	Interview public (sighted Aug 2007); Sin Ming Daily News 15 Oct 2006
27	Changi Creek	Interview public (sighted 2006)
28	Pasir Ris Park	Survey
32	East Coast Recreation Center	Public complaint (May 2007)
39	Bukit Batok Town Park	M. Nasir pers comm. (sighted Dec 2007)
45	Pandan Reservoir	Interview PUB (sighted June 2006)
46	West Coast Park	Nparks staff pers comm. (sighted early 2007)
47	Clementi Woods Park	Nparks staff pers comm. (sighted early 2007)
52	Raffles Place	Radio broadcast (26 July 2007)
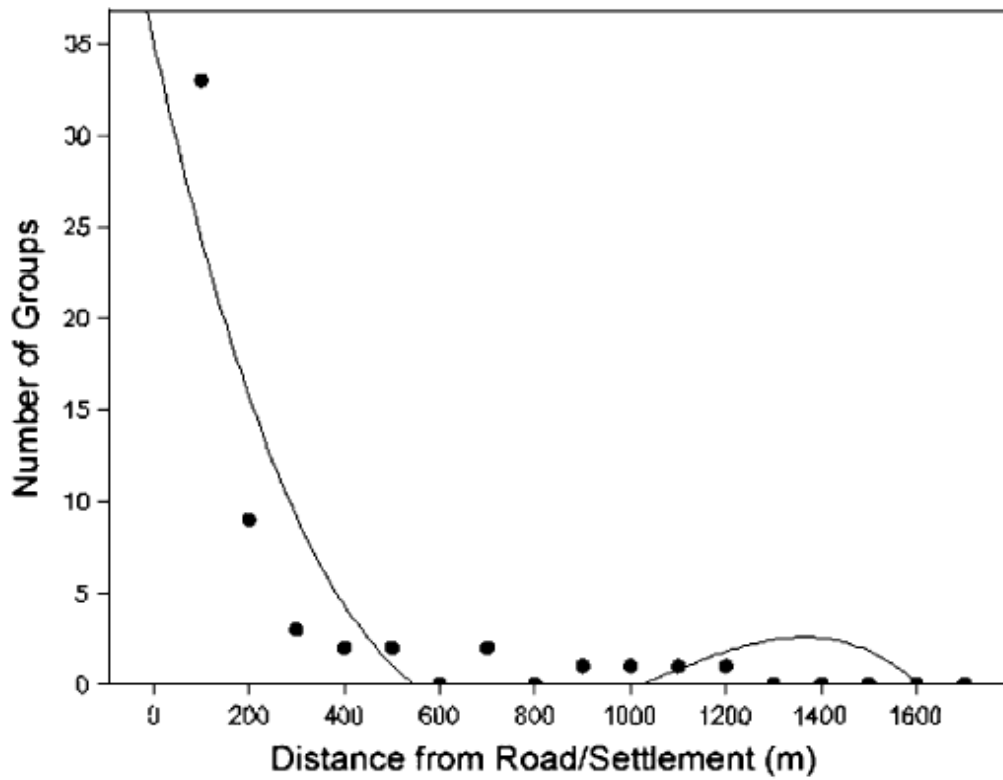
Figure 3: Correlation between the number of macaque groups and proximity to roads and human settlement from the Pearson Correlation and Cubic Regression analysis.
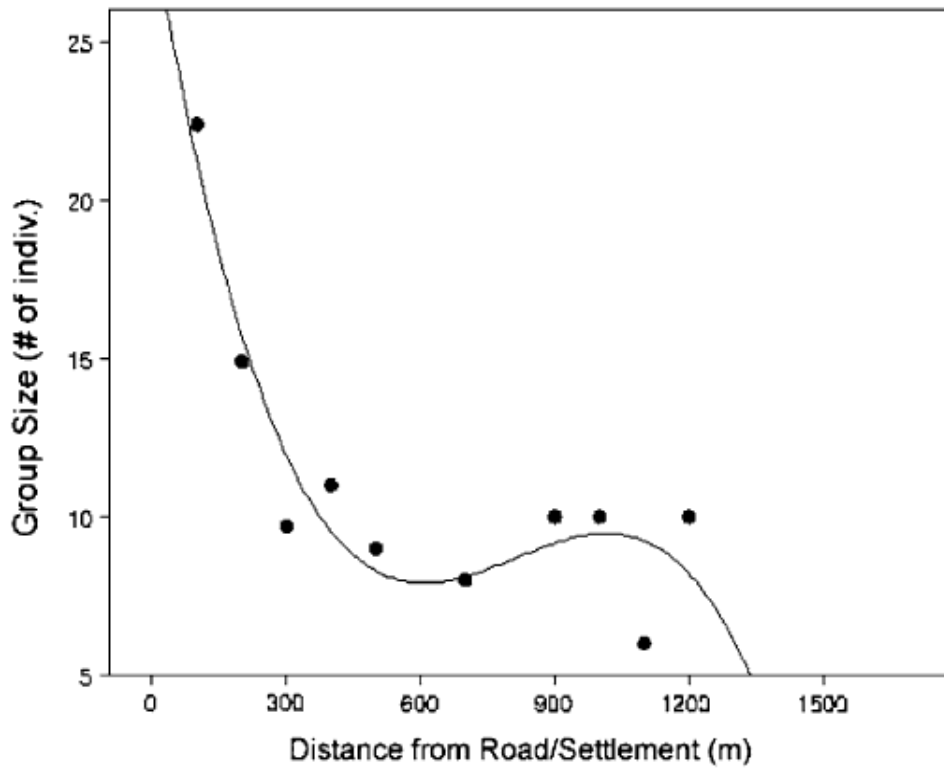
Figure 4: Correlation between group size and distance from road/settlement from the Pearson Correlation and Cubic Regression analysis.
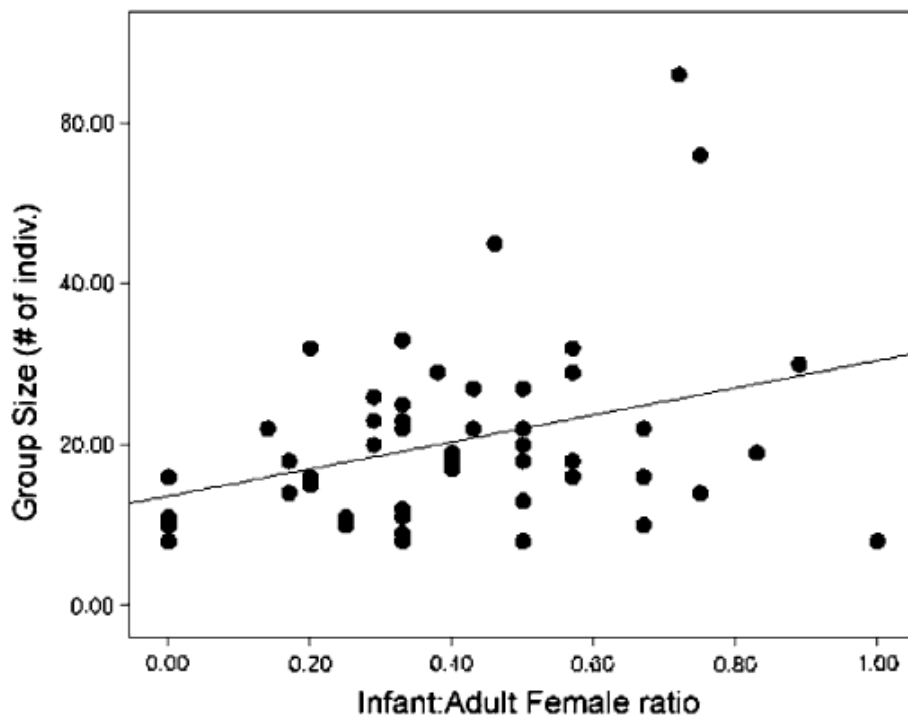
Figure 5: Relationship between group size and infant:adult female ratio from Linear Regression analysis.
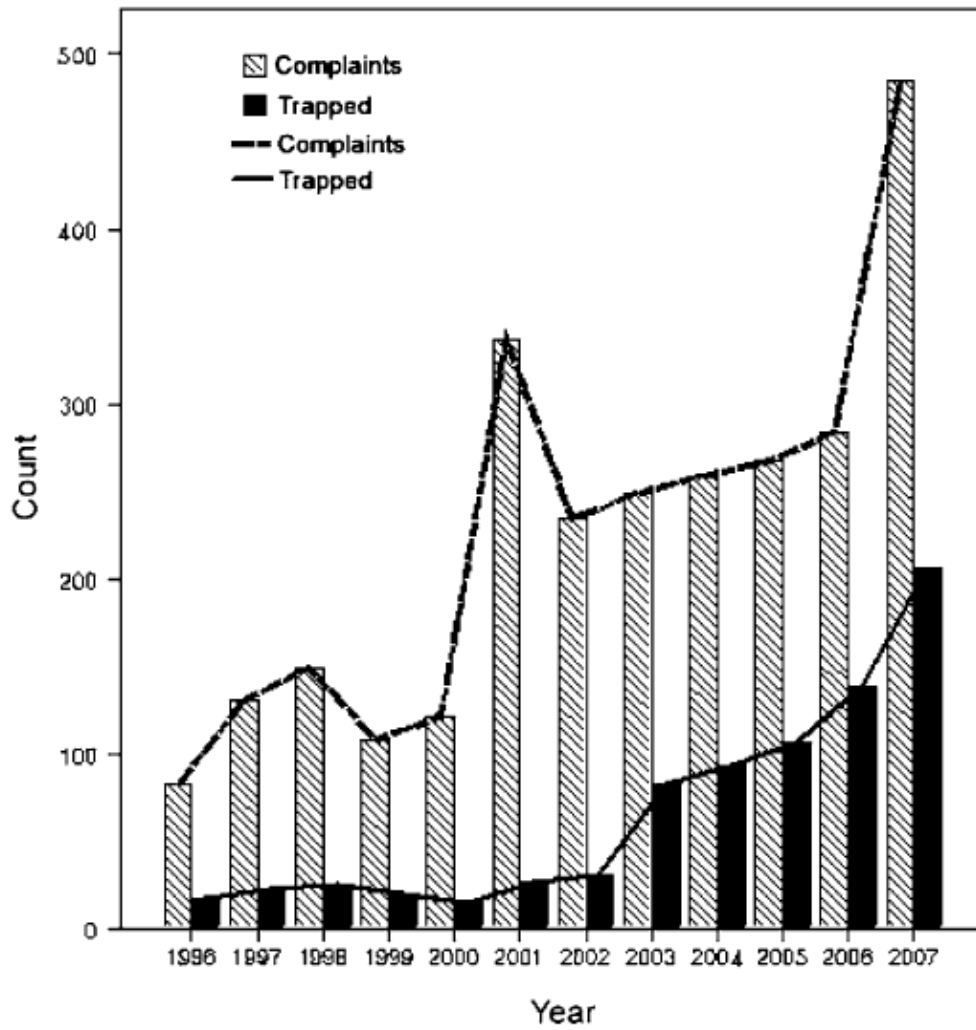
Figure 6: Relation between number of complaints and number of macaques trapped.
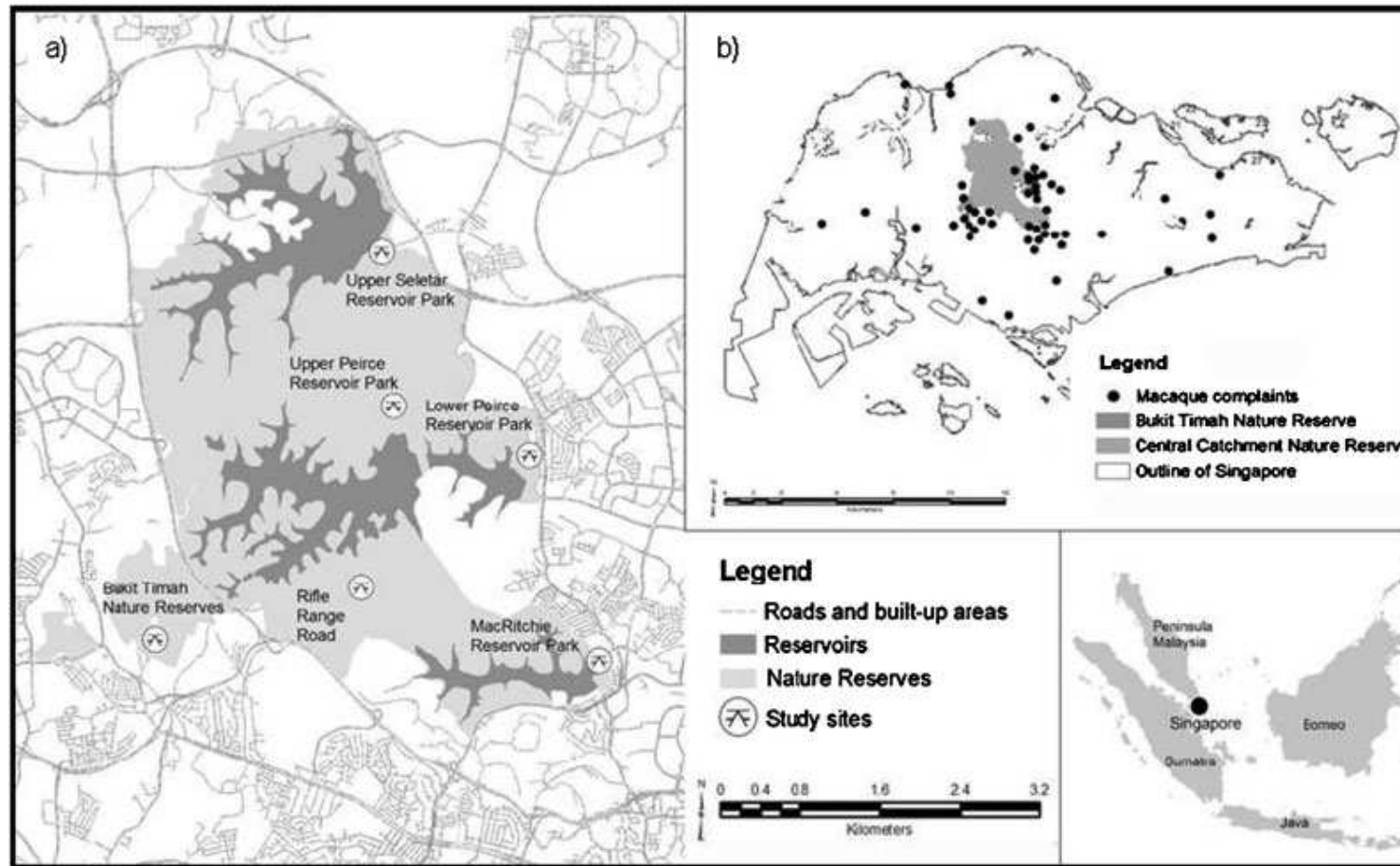
Figure 7: a) The sites of human–macaque interface selected for this study. All sites occurred within Bukit Timah and Central Catchment Nature Reserves and are represented by picnic bench icons. b) The location of public complaints about macaques during 2002–2007 as compiled from Agri-Food and Veterinary Authority (AVA) and National Parks Board (NParks) of Singapore in 2005.

Table 2: Type and frequency of human-macaque interactions at six sites.

| Site	Frequency of interactions per hour of observation (%)								%	Mean[a]
	Scratch or bite	Grab or take	Mobbing	Lunging and chasing	Facial or vocal threats	Affiliative/ Subversive gestures	Physical contact without aggression	Interactions with artificial environment		
Upper Peirce Reservoir Park (UPRP)	0.00	0.71 (28.9%)	0.00	0.33 (13.4%)	0.21 (8.5%)	0.96 (39.0%)	0.08 (3.3%)	0.17 (6.9%)	100	2.46
Rifle Range Road (RRR)	0.00	0.21 (12.6%)	0.04 (2.4%)	0.04 (2.4%)	0.13 (7.8%)	0.96 (57.5%)	0.00 (0.0%)	0.29 (17.3%)	100	1.67
Upper Seletar Reservoir Park (USRP)	0.00	0.21 (8.2%)	0.00	0.21 (8.2%)	0.33 (12.9%)	1.67 (65.6%)	0.00 (0.0%)	0.13 (5.1%)	100	2.54
MacRitchiee Reservoir Park (MRP)	0.00	0.54 (23.5%)	0.04 (1.7%)	0.38 (16.5%)	0.25 (10.9%)	0.67 (29.1%)	0.13 (5.7%)	0.29 (12.6%)	100	2.29
Bukit Timah Nature Reserves (BTNR)	0.00	0.38 (22.5%)	0.00	0.04 (2.5%)	0.13 (7.5%)	0.54 (32.5%)	0.04 (2.5%)	0.54 (32.5%)	100	1.67
Lower Peirce Reservoir Park (LPRP)	0.00	0.13 (8.1%)	0.00	0.13 (8.1%)	0.17 (10.8%)	0.92 (59.5%)	0.00 (0.0%)	0.21 (13.5%)	100	1.55
Mean [b]	0.00	0.36 (17.8%)	0.01 (0.7%)	0.19 (9.2%)	0.20 (9.9%)	0.95 (46.9%)	0.04 (2.1%)	0.27 (13.4%)	100	2.03

[a]Mean frequency of interactions at each site.
[b]Mean frequency of interactions for the behavior category across all observation sites.

Table 3: Interview questions and collated responses in percentage.

Questions (N respondents for question)		Visitors		Residents		Total (Visitors + Residents)		t-statistic [a]	P [b]
		N	%	N	%	N	%		
Attitude towards macaques (507)	Strong or mild liking for macaques	141	36.8	26	21.0	167	32.9	3.386	0.0008
	Neutral	182	47.5	58	46.8	240	47.4	0.155	0.8770
	Strong or mild dislike for macaques	60	15.7	40	32.2	100	19.7	4.012	0.0000
Experienced nuisance problems (512)		96	24.4	86	68.3	182	35.5	5.942	0.0000
Type of problem experienced (182)	Threats, follow/chase	33	34.4	25	29.1	58	31.9	0.820	0.4132
	Theft of items	46	47.9	46	53.5	92	50.5	0.877	0.3816
	Bites or scratches	17	17.7	2	2.3	19	10.5	3.407	0.0008
	Property damage	0	0.0	13	15.1	13	7.1	3.973	0.0001
Perceived cause of problem (411)	Attraction to food	159	53.8	82	71.3	241	58.6	5.178	0.0000
	Natural playfulness	62	20.9	11	9.6	73	17.8	2.721	0.0068
	Provocation by people	61	20.6	15	13.0	76	18.5	1.806	0.0717
	Naturally aggressive	14	4.7	7	6.1	21	5.1	0.580	0.5625
Fed monkeys in past (507)		63	16.4	9	7.3	72	14.2	2.532	0.0116
Will feed monkeys in future (499)		76	20.1	8	6.6	84	16.8	3.484	0.0005
Knowledge of fine (500)		275	72.8	98	80.3	373	74.6	3.093	0.0021
Monkeys do not have enough food in the forest (478)		173	43.9	31	36.9	204	42.7	1.284	0.1999
Do you agree with the effectiveness of feeding ban (495)		305	80.5	87	75.0	392	79.2	2.963	0.032
Knowledge of conflict situation (396)		178	59.9	84	84.8	262	66.2	5.057	0.0000
Problem has to be urgently dealt with (484)		71	19.5	56	46.7	127	26.2	6.211	0.0000
How to manage the macaque problem? (503)	Eradicate macaques	10	2.6	1	0.8	11	2.2	1.185	0.2366

Table 3 Continued

Questions (N respondents for question)	Visitors		Residents		Total (Visitors + Residents)		t-statistic [a]	P [b]
	N	%	N	%	N	%		
Reduce population	29	7.6	26	21.5	55	10.9	4.309	0.0000
Remove nuisance monkeys	4	1.0	7	5.8	11	2.2	3.170	0.0016
Keep nuisance monkeys away from urban areas	82	21.5	24	19.8	106	21.1	0.638	0.5235
Education on co-existence with macaques	257	67.3	63	52.1	320	63.6	3.953	0.0001
Important to conserve and afford more protection to macaques (395)	245	88.1	101	87.1	346	87.6	0.276	0.7823

[a] t-statistic for independent t-tests of difference between visitors and residents for each response.
[b] Significance level at 95% confidence interval.

Table 4: Recorded Macaque related feedback to NParks from Jan to Oct 2007.

Date	Location	Feedback Remarks	Location classified[a]	Behavior classified[b]
10-Jan-07	Casuarina Road	Monkeys from Lower Peirce Reservoir Park roaming into terraces (through backyard) to steal food over the last 3 weeks	NRP	EP
16-Jan-07	Meng Suan Road	Monkey nuisance - request for trap to be set up	NRP	GN
25-Jan-07	Admiralty Road	Monkeys losing their habitat due to construction of Republic Polytechnic are forced to roam into residential area. People are feeding them and the monkeys became aggressive, start to snatch food and might have the possibility of future attacks on people. The authority should look into planning before development. The remaining forest should be conserved before all native plants and animals become extinct.	UPP	GT
21-Feb-07	Springleaf Ave	Monkeys feeding on banana plant in garden. Requested more banners and educational brochures to educate the residents.	NRP	EP
21-Feb-07	Lower Peirce Reservoir Park	Monkeys and birds are intruding residents' kitchens - stealing food and rummaging bins. Suggest more fruit trees to be planted.	NRP	GT
22-Feb-07	East Coast Park	A group of monkeys disturbing children and grabbing people's belongings. Requesting AVA to assist.	UPP	GT
23-Feb-07	Nemesu Ave, Sembawang Hill Estate	Monkeys from Peirce Reservoir Park climbing rooftops to get across to resident's backyards to rummage bins and feed on plants.	NRP	EP
16-Mar-07	Bukit Timah Nature Reserves	Suggested a need for a systematic culling program of monkeys. Lives near Bukit Timah Nature Reserves and monkeys are a definite menace.	NRP	GN
21-Mar-07	Lakeview estate	Monkeys from MacRitchiee Reservoir intruding estate and resident's units. Has sent residents advise not to feed monkeys. Is there a way to deter the monkeys from entering estate?	NRP	EP
17-Apr-07	Beauty World complex	Monkeys from the forest crossing pedestrian bridge, grimacing at people and snatching their belongings. Morning and evening. Daily basis.	NRP	GT
30-Apr-07	Upper Peirce Reservoir Park	Food snatching monkeys	NRP	GT

Table 4 Continued

Date	Location	Feedback Remarks	Location classified[a]	Behavior classified[b]
7-May-07	Jalan Pelatina	At least 20 monkeys are sitting along the steps (needed by residents) in the vicinity of Jln Pelatina. These monkeys can be seen every Sunday. Can authority do something to rid these monkeys into the areas less used by residents.	NRP	S
10-May-07	Windsor Park	Report of many monkeys in the area. Twice entered my house, tried to jump at us instead of going out. Several mornings last week counted over 25 monkeys in my neighbor's garden! Monkeys spill over the dustbins and dirty the place. Already aware that we shouldn't leave any food at reach but is there any other recommendation you can do?	NRP	EP
21-May-07	Bukit Timah Nature Reserves	Increase signage and step up enforcement around residential areas - monkeys are staying longer, getting bolder and attacking members of the public. It is a threat to children.	NRP	A
22-Jun-07	British Club	3-4 different troops frequenting the compound. Requested Zoo to assist with darting, after which AVA will arrange for euthanasia.	NRP	GT
27-Jun-07	SICC golf club	Monkey attacks. Ask for suggestion.	NRP	A
29-Jun-07	Marigold Drive	Taking their food everyday in the late morning till early afternoon	NRP	GT
2-Jul-07	Peirce View Condo	Drivers along Old Upper Thomson Road had been feeding monkeys. Monkeys are venturing out from the nature reserves and foraging for food in the condo. Also swim in the pool. Monkeys getting daring & posing danger to children in the vicinity. Had advice from Nparks but efforts have been futile.	NRP	GT
9-Jul-07	Nemesu Ave	Banana tree in courtyard. Many monkeys	NRP	EP
13-Jul-07	Payar Lebar Airbase	Spotted 3 macaques - worry about safety of personnel and operations. Request for solution.	UPP	S
28-Jul-07	Gladiora Srive	5-6 monkeys found in front of house and in the area.	NRP	S
6-Aug-07	Aam Drive	Too many monkeys coming out of MacRitchiee and roaming in the area. Wants monkeys trapped.	NRP	S
21-Aug-07	Taman Permata	Big troupe of monkeys intruding from MacRitchiee Reservoir Park. Request for loan of monkey traps.	NRP	EP
Sep 07	Yishun Park	Steal food at Yishun Park	UPP	GT
Sep 07	Bedok Reservoir	Snatching food at Bedok Reservoir Park	UPP	GT

Table 4 Continued

Date	Location	Feedback Remarks	Location classified[a]	Behavior classified[b]
11-Sep-07	Jalan Keria	A monkey in the location and intrude into house.	NRP	EP
13-Sep-07	Le Wood Condo	Monkey snatch foods and plastic at outside condo	NRP	GT
21-Sep-07	Bukit Batok Nature Park	near staircase to main road, about 10 monkeys	UPP	S
1-Oct-07	Upper Seletar	Monkeys attack old man	NRP	A

[a]Location classified – NRP = Nature Reserves periphery; UPP = urban park periphery [b]Behavior classified – A = attack; EP = enter property; GN = general nuisance; GT = grab or take; S = sighting of macaque.

Table 5: News headlines.

News Headline	Publisher	Date
Monkeys in Singapore	Lian He Morning News	17 Jan 04
Monkey miracle in Bukit Timah	Shin Min Daily News	31 Jan 04
Hungry monkeys a threat to trail users	Today	10 Feb 04
Macaques aggressive, don't feed the monkeys	Streats	10 Feb 04
Monkey woes at air force base	New Straits Times	26 July 04
200 wild monkeys obstruct traffic waiting for a feed	Shin Min Daily News	5 Oct 04
3 monkeys killed by car in Bukit Timah,	Shin Min Daily News	21 Jan 05
Monkeys in Taiwan and Singapore carry "deadly virus"	Lian He Morning News	7 Jun 05
Look, don't touch. Those fluffy monkeys can deliver a nasty bite	The Straits Times	9 Aug 05
Public urged not to feed wild monkeys	The Straits Times Forum	31 Jan 06
Despite all the warnings, people continue to feed the monkeys	The Straits Times Forum Online	17 Feb 06
Feeding animals in the wild risky	The Straits Times	10 Mar 06
A monkey's letter to Singaporeans	Lian He Morning News	12 Mar 06
Passers-by stopped by wild monkeys in Jurong East	Shin Min Daily News	24 May 06
Monkeys entry house to 'rob' for food	The Straits Times	19 Sep 06
Take action on motorists who feed monkeys at Upper Peirce Reservoir	The Straits Times Forum	27 Sep 06
Undergrad suffers brain injury after monkeys cause crash	The Straits Times	1 Oct 06
Monkeys creating havoc at Windsor Park estate	The Straits Times Online	3 Oct 06
Step up patrols to stop people feeding the monkeys	The Straits Times Online	4 Oct 06
Monkeys in nature reserve not a threat to people	The Straits Times Online	5 Oct 06
Monkeys in parks are becoming more aggressive	The Straits Times Online	5 Oct 06
Monkey havoc: Man, not animals, the real culprit	The Straits Times Online	7 Oct 06
Argh, monkeys stole my cake	The Straits Times	8 Oct 06
Don't feed monkeys, it does them harm	The Straits Times Online	9 Oct 06
Punish monkey feeders	The Straits Times	14 Oct 06
Monkey found in Ang Mo Kio housing estates	Shin Min Daily News	15 Oct 06
Monkeys torment Bukit Timah residents	The Newpaper	21 Nov 06
Residents at Bukit Timah harassed by monkeys	Lian He Evening News	25 Nov 06
Install CCTV to stop people feeding monkeys	The Straits Times Forum	1 Jan 07
Stressed Singaporeans crack down on thieving monkeys	The Star	19 Feb 07
When feeding monkeys = loving them to death	The Straits Times	21 May 07

Table 5 Continued

| News Headline	Publisher	Date
Wlid monkeys creating nuisance at Toa Payoh	Shin Ming Daily News	26 May 07
Adult male monkey roaming near Pasir Ris canal	Shin Ming Daily News	12 June 07
Monkeys downgrading to heartland	The New Paper	5 July 07
Wild monkeys create nuisance at Woodlands	Shin Ming Daily News	8 July 07
Wild monkeys create nuisance at Woodlands, chasing 2 years old child	Shin Ming Daily News	11 Aug 07
Mother monkey hurt, young monkey wails	Lian He Evening News	9 Sep 07
Incident at Marsiling – wild monkey climbs up car and steals tidbits from store	Shin Ming Daily News	9 Sep 07
Feeding monkeys harm them and does not benefit yourself	Lian He Morning News	9 Sep 07
Monkey mayhem at MacRitchie reservoir.	The Straits Times	29 Dec 07
They're still feeding monkeys	The Straits Times	31 Dec 07
Natural to feed the monkeys? Educated adults should know better	The Straits Times Forum	2 Jan 08
$4,000 fine for feeding monkeys	The Straits Times	24 Jan 08
Feeding monkeys? Fine doubled to 500.	The Straits Times	1 Feb 2008
Monkey Mayhem in Bukit Timah	The New Paper	12 Mar 08
More monkeys caught in AVA traps	The Straits Times	22 Mar 08
How macaques and humans can live together.	The Straits Times	25 Mar 08
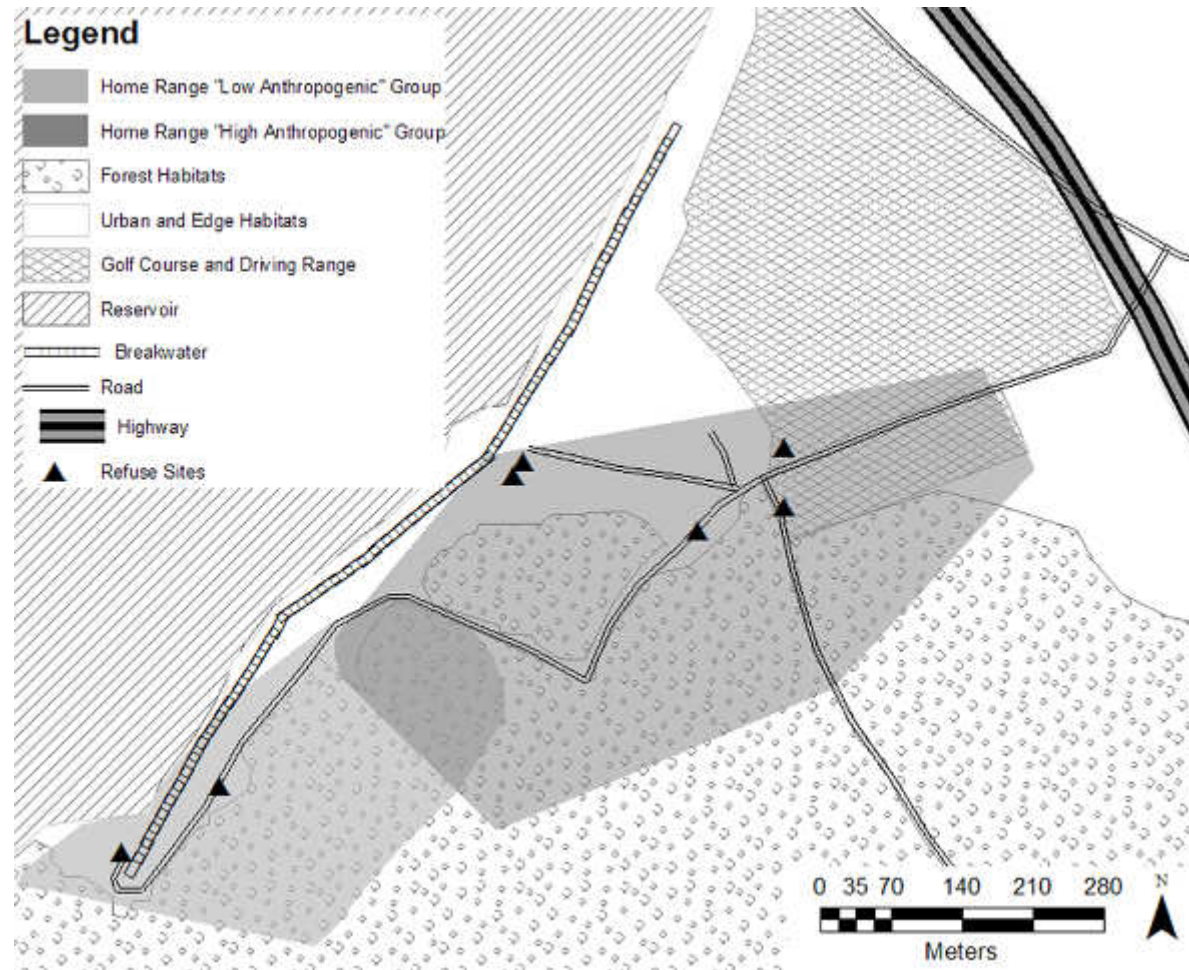
Figure 8: Map of the study area showing major landmarks within the study site, forest and urban/edge habitats, home range of the two study groups and refuse sites within their home range.

Figure 9: Photograph illustrating urban, edge, and forest habitats.

Table 6: Summary of main results for habitat resources, diet, activity, habitat use and ranging for the two study groups of long-tailed macaques. Mean monthly values are shown and where applicable (± SEM, N = 12 months).

	"High Anthropogenic" Group	"Low Anthropogenic" Group
Habitat Resources		
Fruit	22.6 trees/ha	36.9 trees/ha
Flower	14.1 trees/ha	24.0 trees/ha
Young Leaf	247.0 trees/ha	302.1 trees/ha
Refuse (no. of sites with exposed refuse)	1.55 ± 0.08 per day	0.85 ± 0.05 per day
Traffic (no. of humans and cars)	126.7 ± 2.1 per day	94.3 ± 2.4 per day
Diet Composition		
Fruit	20.9 ± 3.1%	74.2 ± 1.7%
Flower	6.3 ± 0.9%	9.7 ± 0.8%
Vegetative Parts	21.0 ± 2.3%	19.6 ± 1.9%
Others	3.4 ± 0.2%	2.5 ± 0.2%
Anthropogenic	48.5 ± 4.5%	25.8 ± 1.1%
Food Plants	36 species	33 species
Activity Budget		
Rest	14.2 ± 2.0%	22.7 ± 1.4%
Locomotion	36.7 ± 1.4%	31.8 ± 2.5%
Feed/Forage	49.1 ± 1.9%	45.5 ± 2.3%
Habitat Use		
Forest	42.0 ± 5.3%	62.7 ± 3.3%
Urban/Edge	58.0 ± 4.3%	37.3 ± 3.2%

Table 6 Continued

	"High Anthropogenic" Group	"Low Anthropogenic" Group
Home Range		
Total	0.182 km^2	0.095 km^2
Mean monthly	0.072 ± 0.007 km^2	0.027 ± 0.002 km^2
Daily Ranging Distance		
Mean monthly	1.80 ± 0.13 km	1.48 ± 0.10 km
Range	1.25 - 2.81 km	1.11 - 2.00 km

Natural resources are presented as mean resource per hectare (±SEM, N = 12 months). Anthropogenic resources are presented as mean resource per day (±SEM, N = 12 months). Diet, activity, and habitat use are presented as mean percentage per month (±SEM, N = 12 months). Percentage diet composition was calculated from scans of feeding activity - mean 67.1 ± SD 5.4 (N = 805) scans per month for the "high anthropogenic" group and 60.3 ± SD 4.3 (N = 724) scans per month for the "low anthropogenic" group. Percentage activity budget and habitat use was calculated from scans of activity and habitat use - 136.8 ± SD 10.4 (N = 1,610) scans per month for the "high anthropogenic" group and 126.4 ± SD 13.6 (N = 1,592) scans per month for the "low anthropogenic" group. Home range is presented as total home range and mean monthly home range (±SEM, N = 12 months) in kilometer square. Daily ranging distance is presented as mean distance per month (±SEM, N = 12 months) in kilometers, with maximum and minimum values. Home range and daily ranging distance were calculated from 11.4 ± SD 1.9 hr per day (N = 410 hr over 36 days) of observation for the "high anthropogenic" group and 11.1 ± SD 2.2 hr per day (N = 398 hr over 36 days) for the "low anthropogenic" group.
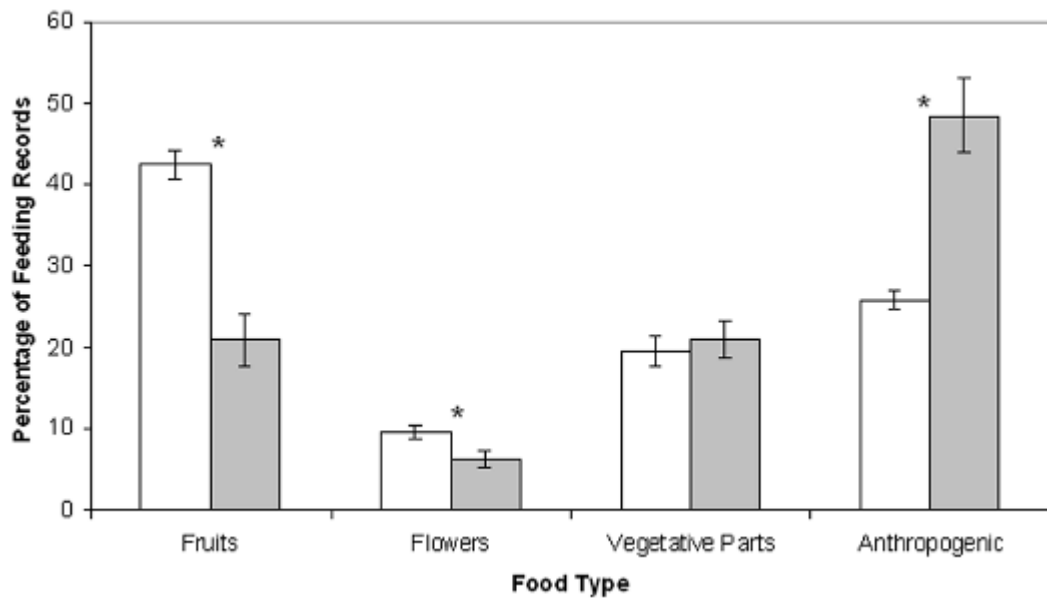
Figure 10: Proportion of time spent feeding on different items for the two study groups. White bars indicate "low anthropogenic" group, grey bars indicate "high anthropogenic" group. Percentages are based on scans of feeding activity-mean 67.1 ± SD 5.4 (N = 805) scans per month for the "high anthropogenic" group and 60.3 ± SD 4.3 (N = 724) scans per month for the "low anthropogenic" group. Columns show mean monthly values (±SEM, N = 12 months). Asterisks indicate significant differences between the two groups (see text for statistics).
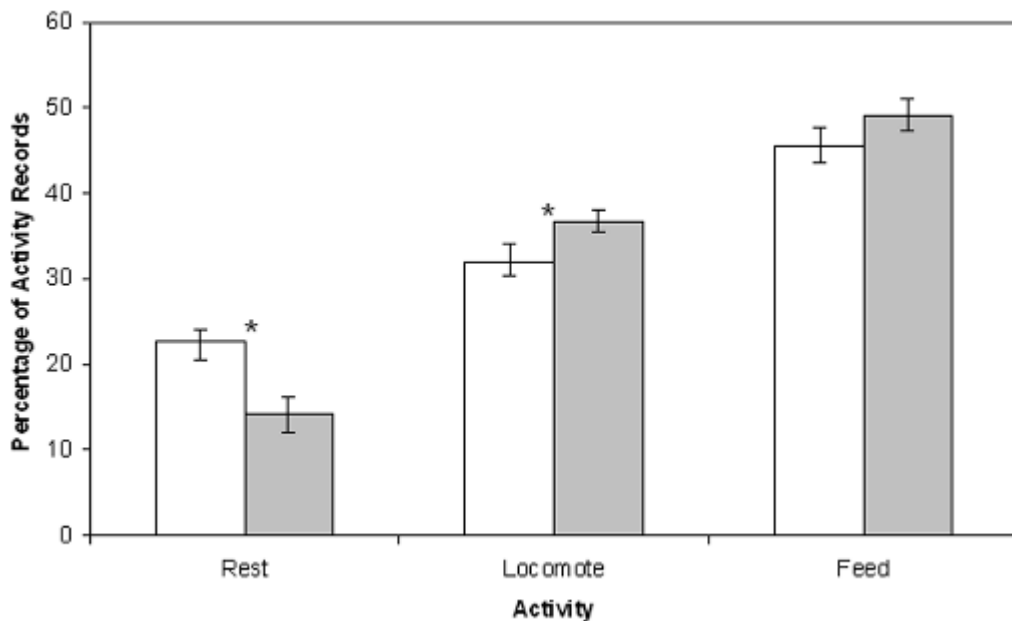

Figure 11: Activity budget of the two study groups. White bars indicate "low anthropogenic" group, gray bars indicate "high anthropogenic" group. Percentages are based on all activity records-136.8 ± SD 10.4 (N = 1,610) scans per month for the "high anthropogenic" group and 126.4 ± SD 13.6 (N = 1,592) scans per month for the "low anthropogenic" group. Columns show mean monthly values (±SEM, N = 12 months). Asterisks indicate significant differences between the two groups.
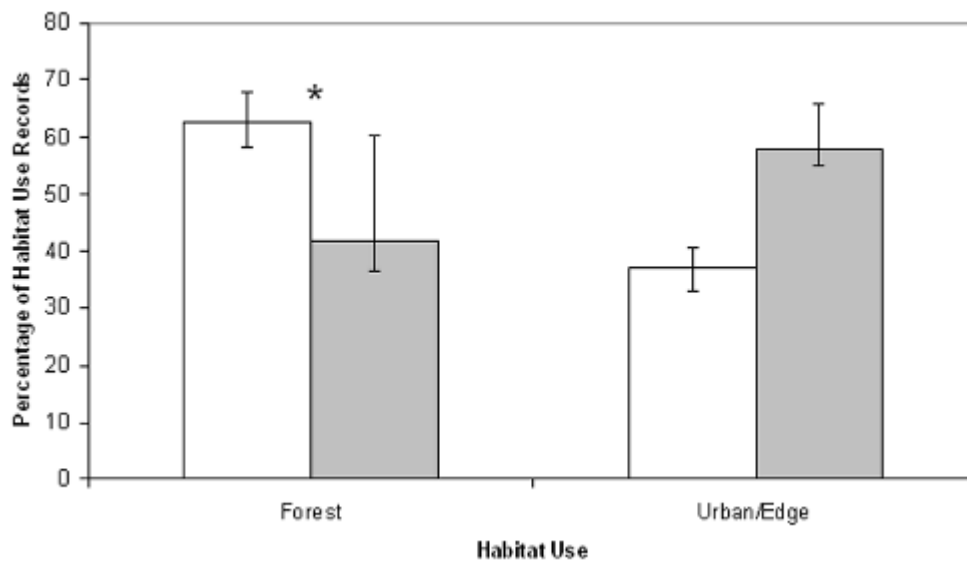
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Figure 12: Habitat use of the two study groups. White bars indicate"low anthropogenic" group, gray bars indicate "high anthropogenic" group. Percentages are based on all habitat use records $136.8 \pm$ SD 10.4 (N = 1,610) scans per month for the "high anthropogenic" group and $126.4 \pm$ SD 13.6 (N = 1,592) scans per month for the "low anthropogenic" group. Columns show mean monthly values ($\pm$SEM, N = 12 months). Asterisks indicate significant differences between the two groups.

Table 7: Food plant species eaten by the two macaque groups.

Species	Parts eaten	Status	Habitat	Mean % consumption by "High Anthropogenic" Group	Mean % consumption by "Low Anthropogenic" Group
Annonaceae					
Cyathocalyx ramuliflorus (Maingay ex Hook.f. & Thoms.) Scheff.	F	Native	Forest	<0.1	0.2
Arecaceae					
Caryota mitis Lour.	F	Native	Forest	0.3	
Oncosperma tigillarium	F	Native	Forest	0.2	
Apocynaceae					
Alstonia angustifolia Wall. ex A. DC	F; Fl	Native	Forest		0.4
Arecaceae					
Elaeis guineensis Jacq.	F	Exotic	Forest		11.8
Ptychosperma macarthurii (H. Wendl. ex anon.) H. Wendl. ex Hook. f.	F	Exotic	Edge	4.2	12.2
Cannabaceae					
Gironniera nervosa Planch.	F; L	Native	Forest	6.8	1.5
Combretaceae					
Terminalia catappa L.	F	Native	Edge	5.6	
Celastraceae					
Bhesa paniculata Arn.	F	Native	Forest		0.3
Clusiaceae					
Garcinia forbesii King.	F	Native	Forest		0.9
Garcinia nigrolineata Planch. ex T. Anderson	F	Native	Forest		0.2
Elaeocarpaceae					
Elaeocarpus petiolatus (Jack) Wall.	F	Native	Forest	7.6	6.2
Ebenaceae					
Diospyros oblonga	F; Fl	Exotic	Forest	2.7	

Table 7 Continued

Species	Parts eaten	Status	Habitat	Mean % consumption by "High Anthropogenic" Group	Mean % consumption by "Low Anthropogenic" Group
Euphorbiaceae					
Blumeodendron tokbrai (Blume) Kurz.	F	Native	Forest	1.7	
Fabaceae					
Archidendron clypearia (Jack) I. C. Nielsen.	L	Native	Forest		0.6
Baphia nitida Lodd. et al.	Fl; L	Exotic	Edge	3.5	2.1
Peltophorum pterocarpum (DC.) Backer ex K. Heyne	L	Native	Edge	4.3	
Pithecellobium dulce (Roxb.) Benth	L	Exotic	Edge	6.2	
Fagaceae					
Lithocarpus elegans (Blume) Hatus. Ex Soepadmo	F	Native	Forest		0.6
Graminae					
Axonopus compressus	S	Exotic	Edge	5.7	
Hypericaceae					
Cratoxylum arborescens (Vahl) Blume.	L	Native	Forest	0.1	
Lauraceae					
Cinnamomum iners Reinw.	L	Native	Forest	0.8	1.1
Litsea grandis Hook. f.	F; Fl	Native	Forest	0.9	0.8
Nothaphoebe umbelliflora (Blume) Blume.	F; L	Native	Forest	4.0	5.2
Malvaceae					
Neesia malayana Bakh.	F	Native	Forest	0.4	
Meliaceae					
Dysoxylum cauliflorum Hiern.	F	Native	Forest	0.2	<0.1
Swietenia macrophylla King	F	Exotic	Edge		0.8
Moraceae					
Artocarpus elasticus Reinw. ex Blume.	F; L	Native	Forest	0.3	
Artocarpus lacucha	F		Edge		0.3

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Table 7 Continued

Species	Parts eaten	Status	Habitat	Mean % consumption by "High Anthropogenic" Group	Mean % consumption by "Low Anthropogenic" Group
Ficus fistulosa Reinw. ex Blume.	F; L	Native	Forest	3.8	1.8
Streblus elongatus Miq.	F; Fl; L	Native	Forest		0.4
Myristicaceae					
Knema malayana Warb.	F;L	Native	Forest	7.6	4.1
Myrtaceae					
Eugenia foetida	F; Fl; L	Native	Forest	0.8	
Rhodamnia cinerea Jack.	F; Fl; L	Native	Forest	7.4	8.3
Syzygium borneense (Miq.) Miq.	F; Fl; L	Native	Forest		3.8
Syzygium grande (Wight) Walp.	F; L	Native	Forest		4.6
Sygygium lineatum(DC.) Merr. & L.M. Perry.	F; Fl; L	Native	Forest		6.5
Syzygium papillosum (Duthie) Merr. & L.M. Perry.	Fl; L	Native	Forest	<0.1	
Phyllanthaceae					
Aporosa frutescens Blume.	F; Fl	Native	Forest	4.7	5.3
Baccaurea bracteata Müll. Arg.	F	Native	Forest	1.9	
Rhizophoraceae					
Gynotroches axillaris Blume.	F	Native	Forest	3.4	1.3
Pellacalyx axillaris Korth.	F; Fl	Native	Forest	0.6	
Rosaceae					
Prunus polystachya (Hook. f.) Kalkm.	F; L	Native	Forest	7.6	15.8
Rubiaceae					
Aidia wallichiana Wall.	L	Native	Forest		0.2
Porterandia anisophylla (Jack ex Roxb.) Ridl.	F	Native	Forest	3.4	1.8
Timonius wallichianus (Korth.) Valeton.	F; L	Native	Forest	0.5	0.7
Rutaceae					
Glycosmis chlorosperma var.chlorosperma	F; L		Forest	<0.1	

Table 7 Continued

Species	Parts eaten	Status	Habitat	Mean % consumption by "High Anthropogenic" Group	Mean % consumption by "Low Anthropogenic" Group
Sapindaceae					
Nephelium lappaceum	F; Fl	Native	Forest	0.8	
Unidentified spp. 1	L	Exotic	Edge		<0.1
Unidentified spp. 2	L	Exotic	Edge		<0.1
Unidentified spp. 3	L	Exotic	Edge	1.8	

Parts eaten – F = Fruit; Fl = Flowers; L = Leaves
Status – Native=Species that have originated in a given area without human involvement or have arrived there without intentional or unintentional intervention of humans from an area in which they are native. Exotic = Species whose presence is a result of either intentional or unintentional human involvement. Classifications follow Chong et al. (2009).
Habitat – Forest and Edge as explained in-text.
Mean percentage consumption - calculated from total counts of feeding recorded on a plant species divided by the total counts of feeding, where plant species was recorded –-N = 3413 for the "high anthropogenic" group and N = 4842 for the "low anthropogenic" group. Blank indicates that no feeding records for the particular plant species were recorded for the group.

Table 8: Spatial distribution (Morisita's Index of Dispersion (I_d) of feeding activity and home range use of the two study groups. Mean monthly values ($\pm$ SEM, N=12 months) are shown. Higher values indicate more clumped spatial distribution on the 20m x 20m scale we assessed.

Factor	"High Anthropogenic" group	"Low Anthropogenic" group	Statistical difference (Paired t-test)
Feeding activity	0.61 ± 0.06	0.75 ± 0.05	Sig (t=2.31, df=11, p=0.041)
Feeding activity in forest habitats	0.42 ± 0.04	0.61 ± 0.06	Sig (t=2.53, df=11, p=0.028)
Feeding activity in urban/edge habitats	0.63 ± 0.07	0.74 ± 0.09	Sig (t=2.45, df=11, p=0.032)
Home range use	0.69 ± 0.08	0.82 ± 0.06	Sig (t=2.49, df=11, p=0.030)
Home range use in forest habitats	0.51 ± 0.10	0.67 ± 0.08	Sig (t=2.36, df=11, p=0.038)
Home range use in urban/edge habitats	0.46 ± 0.03	0.56 ± 0.05	Not Sig (t=2.12, df=11, p=0.058)
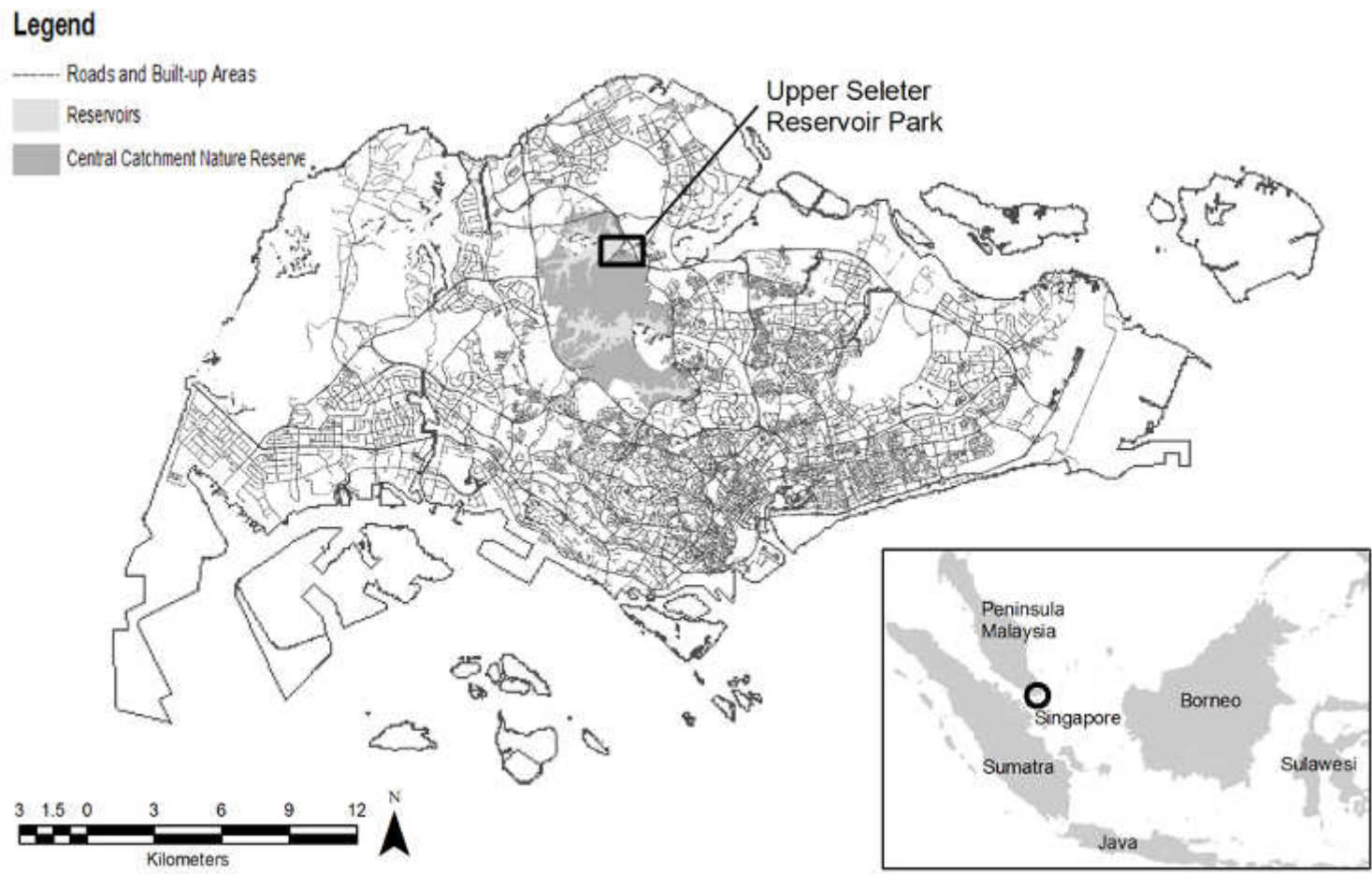
Figure 13: Map of study area.
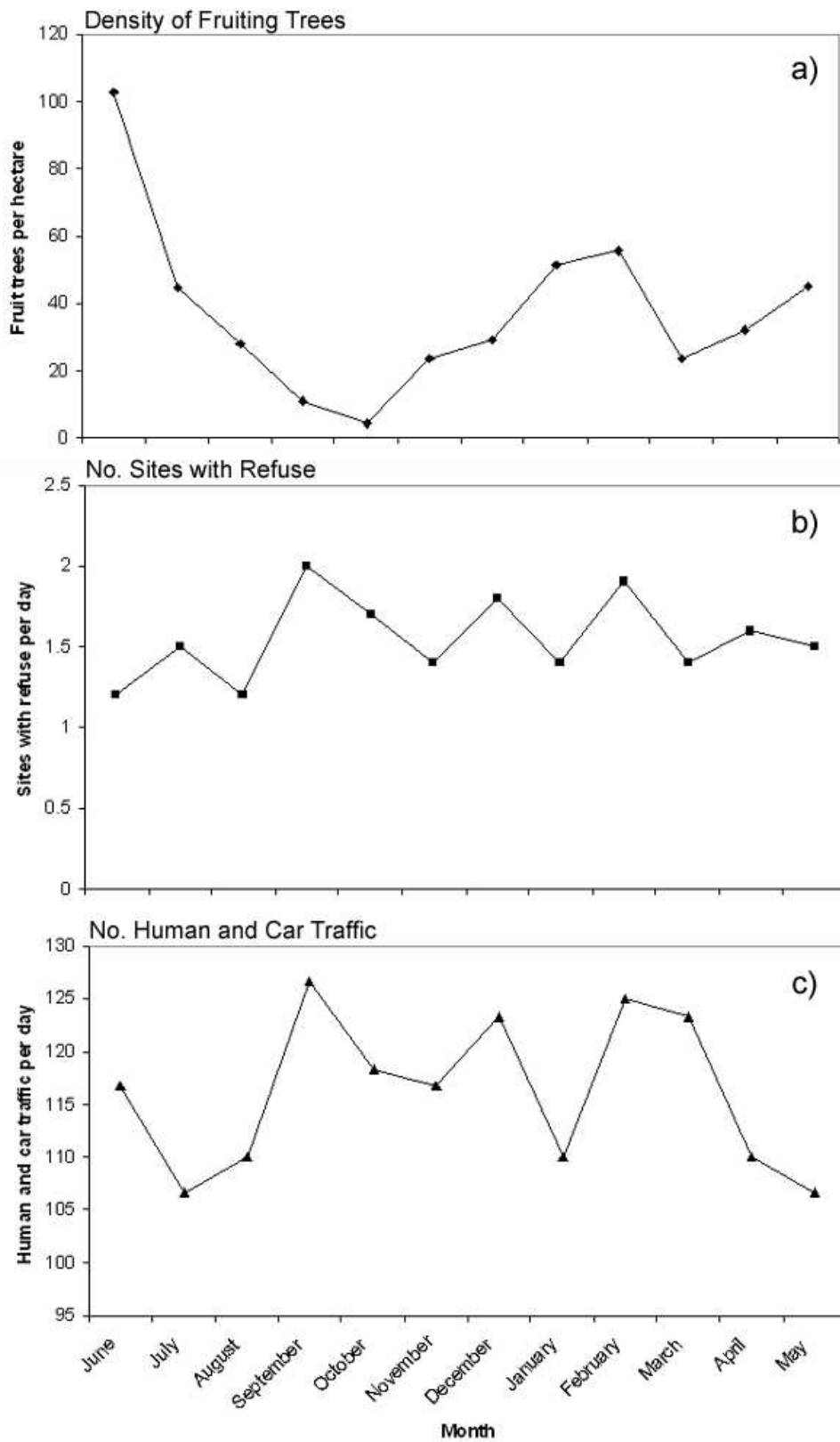
Figure 14: Seasonal trends of a) fruit availability; b) refuse sites with exposed refuse; c) human and car traffic within the "high anthropogenic" group's home range.
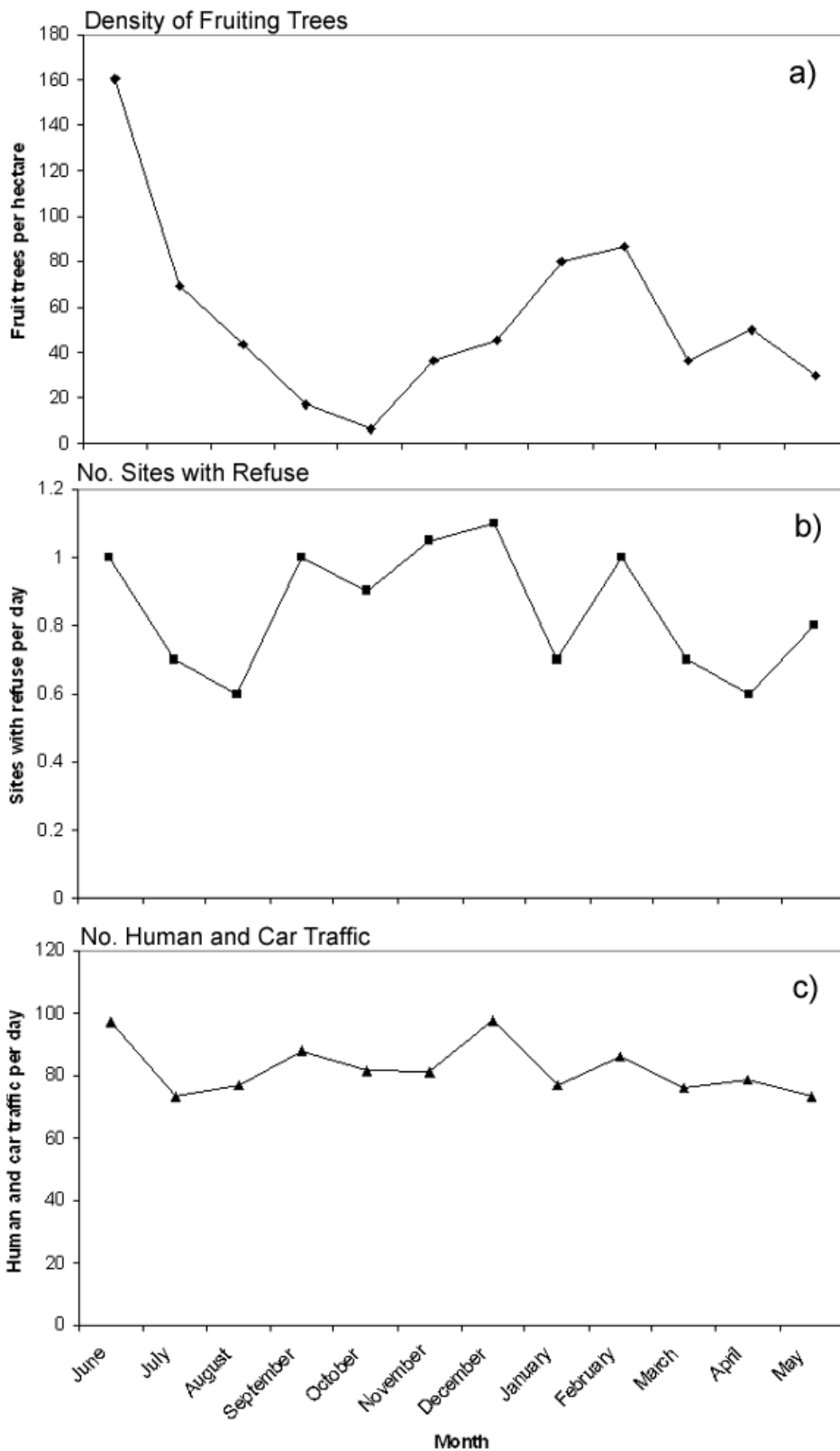
Figure 15: Seasonal trends of a) fruit availability; b) refuse sites with exposed refuse; c) human and car traffic within the "low anthropogenic" group's home range.
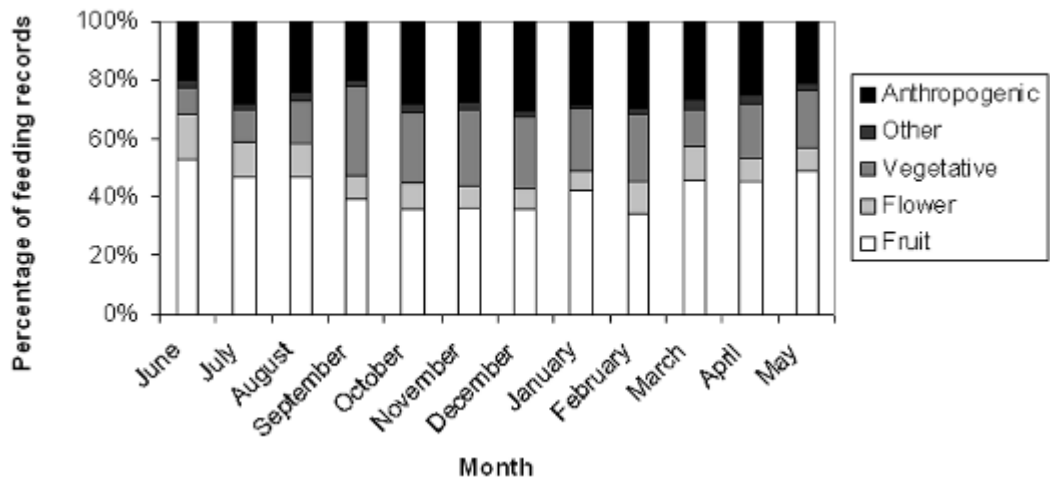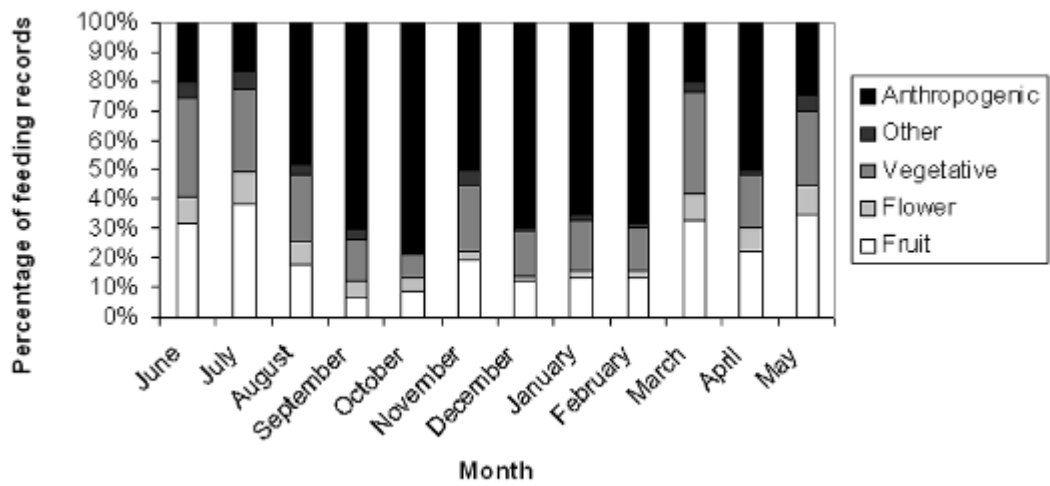
Figure 16: Temporal trends of the macaque diet: a) "high anthropogenic" group; b) "low anthropogenic" group.

Table 9: General Linear Model on the effect of seasonal fruiting, human and car traffic and refuse availability on diet.

a) The effect of fruiting seasonality, human and car traffic and refuse availability on the "high anthropogenic" group's proportion of time spent on fruit feeding $R^2 = 0.636$, df = 11, $P = 0.036$.

Independent factors	Coefficient	SE	t	P
(Intercept)	54.225	41.714	1.300	0.230
Fruit	2.501	1.042	2.400	0.043
Traffic	-0.260	0.339	-0.651	0.533
Refuse	-8.651	11.853	-0.730	0.486

b) The effect of fruiting seasonality, human and car traffic and refuse availability on the "low anthropogenic" group's proportion of time spent on fruit feeding $R^2 = 0.656$, df = 11, $P = 0.029$.

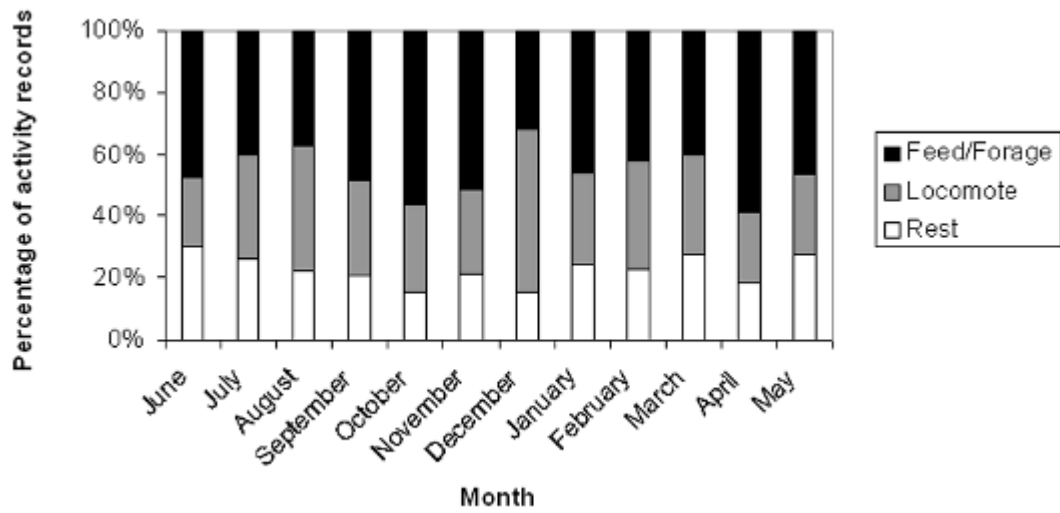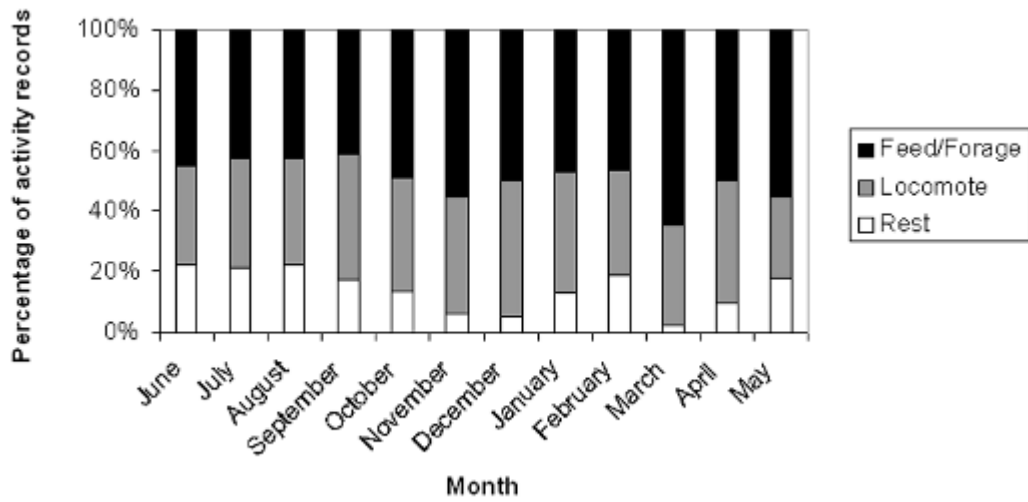| Independent factors	Coefficient	SE	t	P
(Intercept)	48.114	14.059	3.422	0.009
Fruit	1.067	0.405	2.638	0.030
Traffic	-0.003	0.270	-0.040	0.969
Refuse	-13.315	12.389	-1.075	0.314

Figure 17: Temporal trends in activity of a) "high anthropogenic" group; b) "low anthropogenic" group.

Table 10: General Linear Model on the effect of fruiting seasonality, human and car traffic and refuse availability on activity.

a) The effect of fruiting seasonality, human and car traffic and refuse availability on "low anthropogenic" group's proportion of time spent resting $R^2 = 0.802$, df = 11, P = 0.003.

Independent factors	Coefficient	SE	t	P
(Intercept)	43.452	8.547	5.084	0.001
Fruit	1.338	0.993	5.440	0.001
Traffic	-0.523	-0.900	-3.180	0.013
Refuse	16.407	7.531	2.179	0.061

b) The effect of fruiting seasonality, human and car traffic and refuse availability on "high anthropogenic" group's proportion of time spent locomoting $R^2 = 0.620$, df = 11, $P = 0.043$.

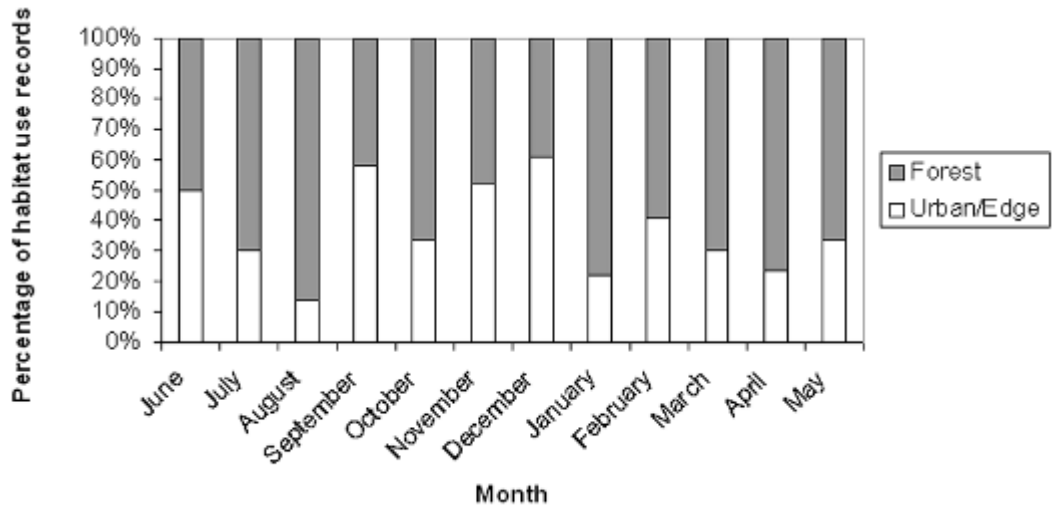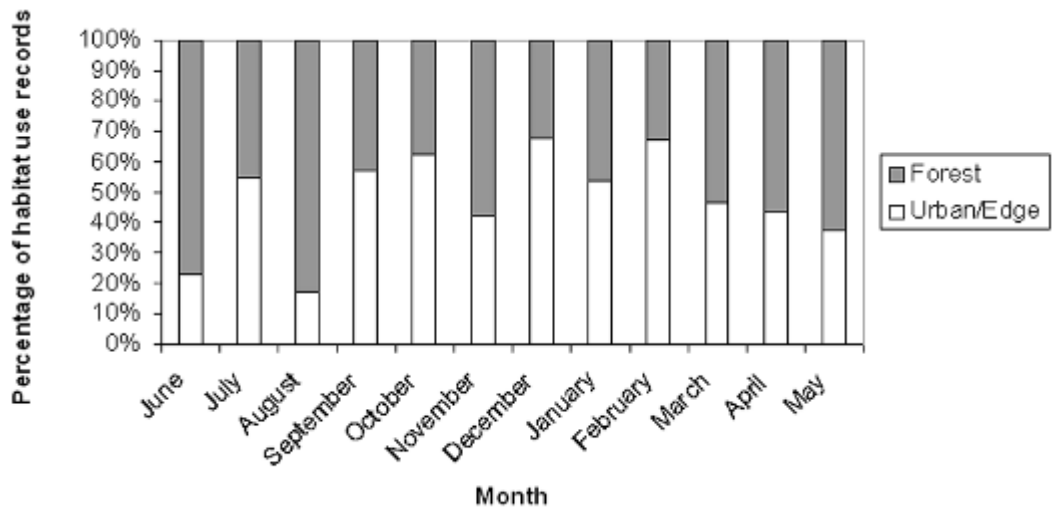| Independent factors	Coefficient	SE	t	P
(Intercept)	-13.432	18.126	-0.741	0.480
Fruit	-0.392	0.453	-0.867	0.411
Traffic	0.466	0.173	2.685	0.028
Refuse	-1.493	5.151	-0.290	0.779

Figure 18: Temporal trends of habitat use for a) "high anthropogenic" group; b) "low anthropogenic" group.

Table 11: General Linear Model on the effect of fruiting seasonality, human and car traffic and refuse availability on habitat use.

a) General Linear Model on the effect of fruiting seasonality, human and car traffic and refuse availability on "high anthropogenic" group's habitat use $R^2 = 0.758$, df = 11, $P = 0.008$.

Independent factors	Coefficient	SE	t	P
(Intercept)	-16.051	34.971	-0.459	0.658
Fruit	-0.048	0.874	-0.055	0.958
Traffic	-0.078	0.335	-0.232	0.822
Refuse	38.981	9.937	3.923	0.004

b) The effect of fruiting seasonality, human and car traffic and refuse availability on "low anthropogenic" group's habitat use $R^2 = 0.878$, df = 11, $P = 0.001$.

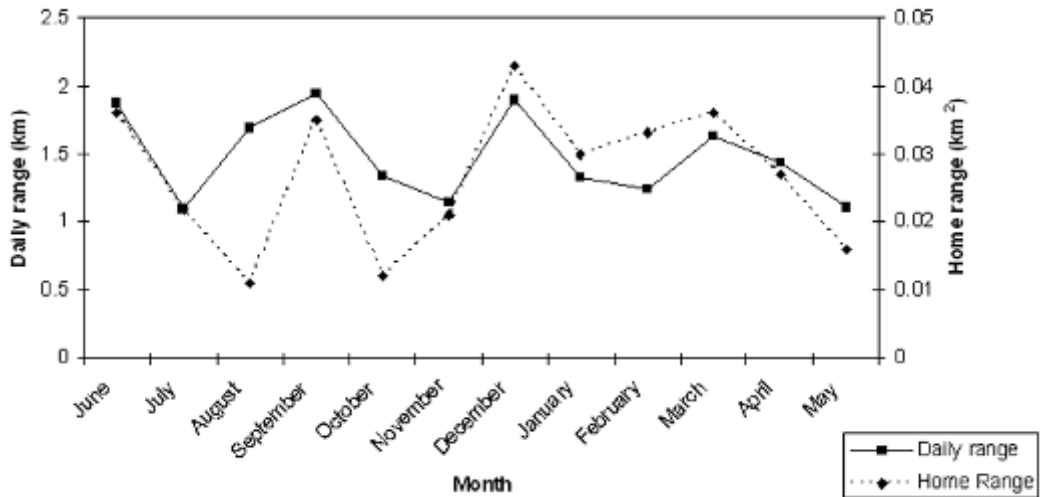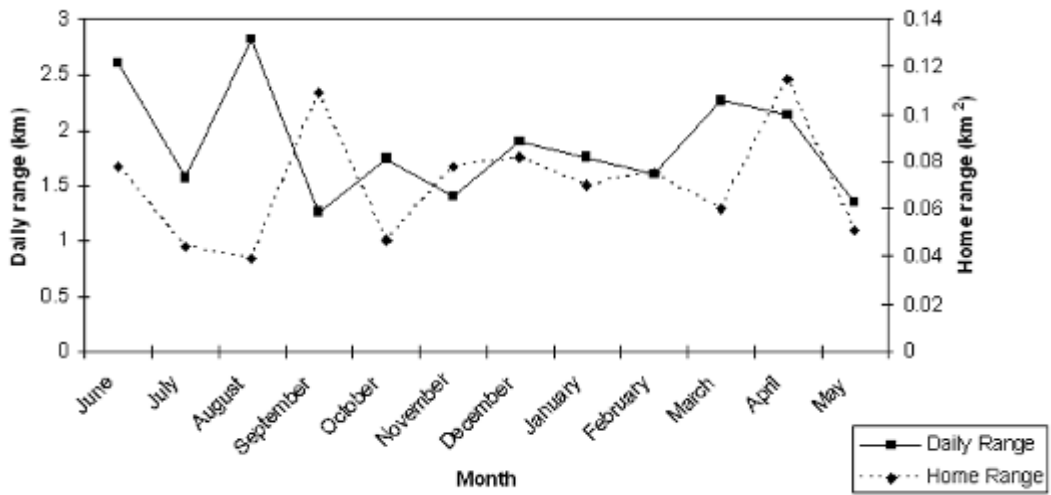| Independent factors	Coefficient	SE	t	P
(Intercept)	-40.994	20.650	-1.985	0.082
Fruit	-0.138	0.595	-0.233	0.822
Traffic	0.283	0.397	0.712	0.497
Refuse	66.128	18.196	3.634	0.007

Figure 19: Temporal trends of ranging patterns for a) "high anthropogenic" group; b) "low anthropogenic" group.

Table 12: General Linear Model on the effect of fruiting seasonality, human and car traffic and refuse availability on ranging.

a) The effect of fruiting seasonality, human and car traffic and refuse availability on "high anthropogenic" group's daily ranging distance $R^2 = 0.523$, df $= 11$, $P = 0.100$.

Independent factors	Coefficient	SE	t	*P*
(Intercept)	0.771	2.172	0.355	0.732
Fruit	0.036	0.054	0.656	0.530
Traffic	0.029	0.021	1.381	0.205
Refuse	-1.539	0.617	-2.493	0.037

b) The effect of fruiting seasonality, human and car traffic and refuse availability on "low anthropogenic" group's daily ranging distance $R^2 = 0.681$, df $= 11$, $P = 0.022$.

Independent factors	Coefficient	SE	t	*P*
(Intercept)	-1.441	0.718	-2.006	0.080
Fruit	-0.10	0.021	-0.506	0.627
Traffic	0.050	0.014	3.653	0.006
Refuse	-1.367	0.663	-2.161	0.063

第 2 章:Sha JCM, Gumert MD, Lee BPYH, Fuentes A, Rajathurai S, Chan S, Jones-Engel L (2009) Status of the long‐tailed macaque Macaca fascicularis in Singapore and implications for management. Biodiversity and Conservation 18(11) 2909-2926. DOI: 10.1007/s10531-009-9616-4

第3章:Sha JCM, Gumert MD, Lee BPYH, Jones-Engel L, Chan S, Fuentes A (2009) Macaque-human interactions and the societal perceptions of macaques in Singapore. American Journal of Primatology 71(10)825-839. DOI: 10.1002/ajp.20710

第 4 章:Sha JCM & Hanya G (2013) Diet, activity, habitat use and ranging of two neighboring groups of food-enhanced long-tailed macaques (*Macaca fascicularis*). American Journal of Primatology 75(6): 581-592. DOI: 10.1002/ajp.22137

第 5 章:Sha JCM & Hanya G (2013) Temporal food resource correlates to the behavior and ecology of food-enhanced long-tailed macaques (*Macaca fascicularis*). Mammal Study 38 (3): 163-175.