Examining how human behaviour and macaque demographics influence the human-macaque (Macaca fascicularis) interface in Singapore

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How to cite:

MARTIN, JOAN HONG (2024) Examining how human behaviour and macaque demographics influence the human-macaque (Macaca fascicularis) interface in Singapore. Masters thesis, Durham University.

Examining how human behaviour and macaque demographics influence the human-macaque (*Macaca fascicularis*) interface in Singapore

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(Author, 2023)

A thesis submitted for the degree of Master of Science by Research in Biological Anthropology

Department of Anthropology
Durham University

January
2024

Examining how human behaviour and macaque demographics influence the human-macaque (*Macaca fascicularis*) interface in Singapore

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Abstract

The increasing presence of anthropogenically altered environments in primate and wildlife populations is leading to more human-wildlife contact. Currently, the literature on primate behaviour in the human-macaque interface predominantly discusses problematic interactions, often referred to as "conflict," neglecting positive relations and human behaviour in interactions. Extensive research on conflict may overemphasize negative aspects of human-macaque interactions making mitigation strategies insufficient to support peaceful coexistence arguments. Further, negativity bias suggesting interactions with macaques are more negative than they are, can hinder conservation success. In this research, I aimed to provide a perspective on the relationship of humans with macaques by analysing behaviours of residents/tourists and long-tailed macaques in encounters at the MacRitchie Reservoir Park in Singapore. I also analysed how macaque sex/age differences based on their life-history traits may influence behaviour and interactions. Of the 2,703 human-macaque encounters observed, I recorded monkeys ignoring humans in 83.17% of the encounters. Only 16.83% of encounters involved macaque-to-human interaction. Most interactions occurred in contexts initiated by humans, especially involving human food (52.31%). Macaques exhibited mostly affiliative/submissive behaviour more than aggressive behaviour in interactions, even when human food was involved. Sub-adult male macaques were involved in most interactions as expected, but adult female macaques were also involved in many interactions more than adult males and juveniles. Humans mostly ignored monkeys (59.79%), while many also appreciated them (33.06%). My findings suggest that humans and macaques mostly live peacefully in Singapore. This may demonstrate that the co-occurrence of humans and macaques is not always a problematic situation requiring interventions. Further, positive psychology can enhance management practices, promoting benefits and identifying mechanisms that make wildlife experiences and protection worthwhile, ultimately optimizing conservation success.

Declaration

I, Joan Hong MARTIN, declare that this thesis titled, "Examining how human behaviour and macaque demographics influence the human-macaque (*Macaca fascicularis*) interface in Singapore" and the work presented in it are my own.

I confirm that this work was done wholly or mainly while in candidature for a research degree at this University. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated. Where I have consulted the published work of others, this is always clearly attributed and acknowledged.

Signed: J H Martin
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Date: 12/1/24
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Examining how human behaviour and macaque demographics influence the human-macaque (*Macaca fascicularis*) interface in Singapore

MARTIN, JOAN HONG

Acknowledgements

I would like to express gratitude to my supervisors Dr. Amanda Tan and Prof. Rachel Kendal for their guidance and feedback, and to field assistant Imogen Simpson for crucial background information. To Prof. Gillian Bentley and Amy Lambton for their invaluable assistance, and to my family and friends for their unwavering support in completing the project. Thank you to my examiners Prof. Joanna Setchell and Prof. Catherine Hill for their helpful comments.

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Chapter 1

Introduction

Wildlife populations are increasingly living in anthropogenically altered environments, leading to greater rates of contact between humans and wildlife. Thus, understanding how and why human and non-human primates (hereafter primates) interact is crucial to fostering coexistence in the Anthropocene epoch (Balasubramaniam et al., 2020). Primates are particularly at risk from overlap with humans due to unsustainable human activities such as habitat loss, bushmeat hunting, illegal trade, and anthroponotic diseases, which are driving them closer to extinction (Estrada et al., 2017). This is particularly true for species that adapt well to anthropogenic environments such as the various macaque species that live in forest edges and near human settlements (Gumert, 2011).

Currently, much of the literature on primates' behaviour in human-macaque interfaces has mainly focused on problematic interactions, particularly in areas where negative interactions are likely, such as places where primate tourism is heavily promoted (e.g., O' Leary and Fa, 1993; Wheatley et al., 1994; Wong and Ni, 2000; Fuentes and Gamerl, 2005; Sabbatini et al., 2005; Sha et al., 2009; Ilham et al., 2018; Radford, Alexander and Waters, 2018). Such negative interactions often involved macaques acquiring human food, through human provisioning or macaque 'theft,' and macaques threatening or scratching humans if food is withheld (O' Leary and Fa, 1993; Wheatley et al., 1994; Wong and Ni, 2000; Fuentes and Gamerl, 2005; Sabbatini et al., 2005; Sha et al., 2009; Ilham et al., 2018; Radford, Alexander and Waters, 2018). These types of negative interactions have often been referred to as "conflict" in literature. Wildlife management often faces constraints due to a focus on negative interactions, neglecting positive relations (Frank, 2016). Although a few scholars have included some positive relations in addition to negative interactions in their studies, these are few (e.g., Sabbatini et al., 2005; Hsu, Kao and Agoramoorthy, 2009; Kaburu et al., 2019).

Coexistence is defined as a dynamic, sustainable state where humans and wildlife adapt to shared environments, with effective human laws governing interactions to safeguard wildlife population longevity while allowing legitimate and tolerable risks to humans (Carter and Linnell, 2016; Mekonen, 2020; Pooley, Bhatia and Vasava, 2020). To promote coexistence and tolerance towards wildlife (Frank, 2016), research should also quantify positive interactions and low interaction levels in human-wildlife interfaces to understand factors that may promote or hinder coexistence, as well as explore interfaces where no interactions occur.

Focusing on interactions conventionally termed “conflict” is also problematic because traditional anthropocentric definitions of human-wildlife conflict overlook the human role, focusing solely on reducing wildlife threats to human safety, interests, and wellbeing (Frank and Glikman, 2019). Although the term “ethnoprimatology” was first coined by Sponsel in 1997, awareness of how humans may affect primates dates back to decades earlier when the importance of field primate studies in anthropology was first recognised (Riley, 2018). In 1955, Sherwood Washburn, a US primatologist, observed baboons adapting to his hotel environment in Victoria Falls during a trip to Africa (De Vore and Washburn, 1992), while in India, assessing the rhesus macaques’ natural habitat was challenging due to their close ecological ties with humans for centuries (Southwick, Beg and Siddiqi, 1965). Further, in Bruce Wheatley's study on the macaques in Bali (1994), the author stresses the need to consider the human cultural context for understanding macaque behaviour. Indeed, human food acquisition is primarily observed within contexts initiated by humans from direct human provisioning (O’ Leary and Fa, 1993; Wheatley et al., 1994; Wong and Ni, 2000; Fuentes and Gamerl, 2005; Sabbatini et al., 2005; Sha et al., 2009; Ilham et al., 2018). This causes predictable feedback loops creating changes in macaque responses, such as aggression (Cox and Gaston, 2018) and inevitably highlights problematic interactions and behaviours. Sponsel and Wheatley emphasize the need to acknowledge humans as part of nature and interpret primate behaviour as ecological strategies, rather than conflict-causing aberrant behaviour (Riley, 2018).

Recognizing humans as a solution for positive human-primate coexistence promotes tolerance and understanding that wildlife and humans can thrive in shared landscapes (Frank and Glikman, 2019). Thus, a comprehensive understanding of the human social and cultural aspects of conservation is also crucial for effective management of the human-primate interface (Setchell et al., 2017). Moreover, extensive research on “conflict” and limited research on benefits may overemphasize negative aspects of human-wildlife interactions (Soulsbury and White, 2015) neglecting positive consequences and making mitigation strategies insufficient to support arguments for peaceful coexistence (Buijs and Jacobs, 2021). Negativity bias suggesting interactions with wildlife are more negative than they really are, can hinder conservation success in wildlife management practices (Buijs and Jacobs, 2021).

Positive psychology theory suggests that human-wildlife interactions can bring happiness and well-being through meaning, engagement, and pleasure (Buijs and Jacobs, 2021). Peaceful coexistence can enhance psychological, physical, and economic wellbeing for humans, primates and other wildlife living together (Wheatley et al., 1994; Cox and Gaston, 2018; Radford, Alexander and Waters, 2018; Mekonen, 2020). With literature focusing on negative outcomes of human-macaque interaction, increasing scholarly output on positive or even neutral interactions and peaceful coexistence, and communicating these findings to communities that live with primates, could enhance conservation success (Frank, 2016; Mekonen, 2020; Konig et al., 2021). Research on human-wildlife interactions that promote positive psychology can reinforce known benefits, reveal unknown ones, and uncover mechanisms that make wildlife experiences and protection meaningful and rewarding (Buijs and Jacobs, 2021).

Further, understanding whether some individuals (more than others) are more likely to initiate interactions with humans, engage in prolonged interactions, and resort to costly behaviours such as aggression towards humans (Balasubramaniam et al., 2020), will help better inform management practices to enhance cohabitation, consider shared benefits (Buijs and Jacobs, 2021), and increase peaceful coexistence (Balasubramaniam et al., 2020). According to life history theory, risk-taking wildlife behaviour is influenced by fitness expectations and energetic requirements and can be observed through intraspecific differences in human resource exploitation (Janson and van Schaik, 2002; Wolf, 2009; Chiyo, Moss and Alberts, 2012; Morrow et al., 2019). Polymorphic populations often arise from the trade-offs between current and future reproduction (Roff, 2002; Rueffler, Van Dooren and Metz, 2004), with some individuals prioritizing future fitness returns over others (Clark and Ehlinger, 1987; Wolf, 2009). Individuals with high future fitness expectations, such as females, may be more risk-averse than those with low future expectations, since they have more to lose (Wolf, 2009). Further, macaque sex/age class differences may also influence human preference to engage with some wildlife individuals more than others (O'Leary and Fa, 1993; Sabbatini et al., 2005).

In this research, I will investigate macaque and human behaviours in interactions observed at the MacRitchie Reservoir Park in Singapore. I will catalogue human behaviour to understand the contexts under which interactions occur and consider factors influencing human and macaque behaviour, such as macaque demographic and life history traits. The types of interactions occurring between humans and macaques will be characterised and the contexts in which these interactions occurred will be identified. I will aim to provide descriptions of all behaviours that occurred when humans and macaques are in proximity of each other, including positive, neutral, and problematic behaviours. I will present this report in several parts, including a review of the literature, my research questions, hypotheses, and predictions. This will be followed by a separate chapter each, for methods, results, discussion, and conclusion.

Chapter 2

Literature Review

Rapid environmental changes are causing wildlife populations, including primates, to increasingly inhabit anthropogenic settings. This often involves direct human influence, such as human provisioning, or indirect human influence, such as habitat destruction (Morrow et al., 2019). Primate research in these settings allows scholars to explore how species have evolved to adapt to current environmental changes (Wong and Candolin, 2015), while also addressing conservation concerns (Morrow et al., 2019). Environmental changes, human behaviour, and growing human population numbers can alter human-primate coexistence patterns, bringing humans and primates closer together due to shared spaces and resources (Frank and Glikman, 2019; Morrow, 2019). Increased human-primate interactions, facilitated by shared landscapes and resources, can lead to beneficial or harmful outcomes for both species (Parathian et al., 2018). For instance, primates may exhibit changes in ecology, movement, and behaviour when consuming anthropogenic food sources, while humans may engage in feeding behaviour in response to animal presence (Morrow et al., 2019). Interactions involving wildlife feeding can enhance human wellbeing by addressing chronic health conditions (Soga and Gaston, 2020), while providing nutrient-rich food to primates, but it can also increase risks of injury, bi-directional disease transmissions, and animal roadkill-related deaths (Sha et al., 2009; Jones-Engel et al., 2011; Morrow et al., 2019; Balasubramaniam et al., 2020).

Primates affected by human activity need not be considered as unnatural or unimportant for studying primate behaviour and evolution (Gumert et al., 2011; Setchell et al., 2017). Indeed, human-wildlife interactions have been a defining feature of human experience and existence since the beginning, as depicted in early cave paintings (Nyhus, 2016). These interactions have influenced human and wildlife cultures, communities, and species evolution, shaping human experience and existence (Nyhus, 2016; Konig et el., 2021). Equally, humans and primates have shared ecosystems for millennia, forming crucial biotic factors of the ecology, impacting each other's evolutionary paths (Gumert et al., 2011; Setchell et al., 2017). Understanding sympatric relationships between humans and primates are crucial for primate ecology, evolution, and conservation (Patterson and Wallis, 2005; Riley, 2010; Gumert et al., 2011; Setchell et al., 2017). Thus, more accurate, and comprehensive documentation and systematic study of the human-primate interface, combining with a bio-social approach (Setchell et al., 2017), is key to understanding human-primate interactions (Fuentes, 2006a/b; Lane et al., 2010; Gumert et al., 2011).

2.1 The growth of human-primate interfaces and the problem with “conflict”

Currently, the literature on primate behaviour in the human-primate interface has focused on negative human-primate interactions (O’ Leary and Fa, 1993; Wheatley et al., 1994; Wong and Ni, 2000; Fuentes and Gamerl, 2005; Sabbatini et al., 2005; Sha et al., 2009; Ilham et al., 2018; Radford, Alexander and Waters, 2018; Balasubramaniam et al., 2020). These interactions often involve primates acquiring human food, through human provisioning and primates threatening, scratching, or biting humans when humans withhold food (O’ Leary et al., 1993; Wheatley et al., 1994; Wong and Ni, 2000; Fuentes and Gamerl, 2005; Sabbatini et al., 2005; Sha et al., 2009; Ilham et al., 2017). The term "conflict" is commonly used to describe such negative human-wildlife interactions, where one or both sides are negatively affected, but this definition may be subject to debate. It suggests that wildlife consciously opposes humans, when they are merely exhibiting natural opportunistic foraging behaviour (Peterson et al., 2010). Critics argue that this term promotes the notion that humans and wildlife are deliberately adversarial (Setchell et al., 2017) and overlooks the positive qualities of human-wildlife relationships (Hill, 2015). On the other hand, conflict may be a result of differences among human ideologies, social groups, and institutions, over the meaning of wildlife and its place in society (Hill 2015; Frank and Glikman, 2019). For instance, some humans feed wildlife, such as primates, causing wildlife to view all humans as food sources, while other humans do not. This often creates "conflict" between groups of humans rather than between humans and wildlife, leading to wildlife suffering, such as primate culling due to public complaints (Sha et al., 2009; Feng, 2015).

Human-wildlife interactions today often arise from humans attempting to separate humans from non-human species, resulting in interactions that may be deemed problematic through the creation of exclusive spaces for humans or wildlife (Frank and Glikman, 2019). Whether physical, such as fences and walls, or figurative, like the wilderness and protected areas (Knight, 2000; Creager and Jordan, 2002; Frank and Glikman, 2019), this idealism of boundaries distance humans from nature, influencing human-wildlife interactions and causing "conflict" over or with wildlife (Ripple et al., 2014; Liordos et al., 2017; Frank and Glikman, 2019). However, in some countries that have lived with wildlife in millennia-old, shared landscapes (e.g., Southwick et al., 1965; De Vore and Washburn 1992; Wheatley et al., 1994; Riley, 2018) or in established wildlife protected areas within human territories, such as in Southern Europe, Asia and Africa (De Vore and Washburn, 1992; O'Leary and Fa, 1993; Wheatley et al., 1994; Sha et al., 2009), there are no such clear boundaries (Frank and Glikman, 2019).

Traditional anthropocentric definitions of human-wildlife conflict often also neglect the human role and focus solely on solutions to reduce wildlife threats to humans (Frank and Glikman, 2019). Recognizing humans as part of nature and interpreting primate behaviour as ecological strategies (Wheatley et al., 1994 and Sponsel, 1997) promotes tolerance and understanding that both humans and primates can coexist successfully in shared landscapes (Frank and Glikman, 2019). Coexistence is a sustainable, dynamic relationship between humans and wildlife, governed by effective human laws to protect wildlife population longevity while allowing legitimate risks to humans (Carter and Linnell, 2016; Mekonen, 2020; Pooley, Bhatia and Vasava, 2020). To accurately assess risks, research should focus on studying all interactions, including the absence of interactions, rather than solely on negative aspects. The literature needs to be updated to promote coexistence, positive interactions, and tolerance towards wildlife to maximize conservation success (Frank, 2016; Mekonen, 2020; Konig et al., 2021). Further, to achieve successful, long-term resolution for a peaceful coexistence, it is crucial to address underlying social conflicts among various human groups before or while applying solutions to problematic human-wildlife interactions (Hill, 2015). Identifying potential mismatches between interfaces and human perceptions can help achieve this aim.

2.1.1 Human-macaque interfaces

Macaques (*Macaca* spp.), a diverse genus of Afro-Eurasian monkeys, are the most widely distributed primate taxon apart from humans (Fa, 1989; Roos and Zinner, 2015) with twenty-three recognised species currently (Riley et al., 2016). Some macaque species and humans share extensive geographical overlap due to common ecological pressures, evolutionary histories, and physiologies, such as simple digestive systems and flexible diets (Gumert et al., 2011). Over the past two million years, human and macaque ancestors successfully migrated from Africa and the Mediterranean basin to South and Southeast Asia, where the largest human and macaque populations are currently found (Hart and Sussman, 2008; Gumert et al., 2011). Barbary macaques (*Macaca sylvanus*) are found in northwestern Africa and Gibraltar, probably introduced by humans, while the other macaque species reside across Asia (Roos and Zinner, 2015), such as the Japanese macaques (*Macaca fuscata*), and Formosan macaques (*Macaca cyclopis*) in Taiwan. The rhesus macaque (*Macaca mulatta*) is the most successful species in India, while the long-tailed macaque (*Macaca fascicularis*) is the most common species in Southeast Asia (Gumert et al., 2011). The types of human-macaque interfaces are varied, but due to ecological and physiological overlaps, macaques tend to inhabit forest fringes and riverine near human settlements (McConkey and Chivers, 2004; Fooden, 2006). Historically and today, macaques elicit diverse experiences among people living near them in interface zones (Hill, 2015). For instance, Japan's rural farming areas face significant damage from macaques, who range into homes and forage on crop and burial offerings, but farmers feed them in winter to alleviate potential suffering due to food shortage (Knight, 2003; Hill, 2015), while heavy provisioning in Hong Kong led macaques to wander into suburbs in search of food in human homes (Jones-Engel et al., 2011).

2.1.2 The long-tailed macaque

Long-tailed macaques may have lived near humans for thousands of years, with evidence from Niah Cave in Sarawak suggesting that around 20,000 years ago, humans and long-tailed macaques interacted (Harrison, 1996; Gumert et al., 2011) Their populations span across Southeast Asia, including Bangladesh, Myanmar, Thailand, Cambodia, Laos, Vietnam, Sundaland, and the Philippines, whilst also inhabiting smaller islands, such as Sumatra, Nicobar Islands, Maratua, and Singapore, among others (Gumert et al., 2011). Fooden (1995) estimated the 1980s long-tailed macaque population in Asia at 5 million, reassessing 11 years later to 3 million (Fooden, 2006). The human-macaque interface is primarily influenced by human behaviour and human activities (Jones-Engel et al., 2011). The long-tailed macaque population in Southeast Asia has been declining due to human activities such as logging, agriculture, habitat destruction, and human population growth (Wheatley et al., 1994; Fooden, 2006). However, a larger proportion of macaques may be interacting with human environments due to their preference for habitats near human settlements (Gumert et al., 2011). Long-tailed macaques are ecologically linked to humans due to their adaptability to human-modified habitats, such as forest edges, riverine environments, and disturbed habitat borders near human settlements (McConkey and Chivers, 2004; Fooden, 2006).

The long-tailed macaques have a long history of cooperation with humans, with both macaques and humans benefiting from their association (Wheatley, et al., 1994; Gumert et al., 2011). For instance, in India and Indonesia, local communities and stakeholders promote tourism and traditional Hindu values, aiming to protect all flora and fauna, especially revered species like monkeys, have enabled monkey populations to thrive. Largely involving human provisioning of macaques, the Monkey Forest of Ubud in Bali, Indonesia, has experienced an increase in their monkey population (Wheatley et al., 1994), with local stakeholders opposing wildlife managers' proposals to cull or relocate macaque individuals to manage overpopulation and increased aggression (Southwick and Siddiqi, 1983; Malik, 1988; Wheatley et al., 1994). Further, tourism significantly contributes to the income of many stakeholders, as most tourists visiting the Monkey Forest visit and feed the monkeys (Wheatley et al., 1994). Macaque populations at provisioning sites tend to increase rapidly, surpassing the natural habitat's capacity to sustain them (Sugiyama, 2015). However, a high macaque population density likely contributes to increased rates of inter-group aggression and infant mortality, helping check population growth (Wheatley et al., 1994). In Bali, India's Aligarh district, and in Tughladqabad, traditional and cultural norms dictate human-macaque relationships. This results in self-sustaining macaque populations, albeit artificially (Sugiyama, 2015). Due to the positive relations between humans and monkeys, their stories may be deemed a conservation success by some scholars (Marsh, 1987; McNeely et al., 1990; Brautigam, 1991).

2.2 Characterising human-macaque interaction

Fuentes et al. (2008) collected data on interaction behaviours and demographics to characterise human-long-tailed macaques interaction patterns in Singapore. The authors reveal that physical contact between humans and macaques is rare, indicating a minimal risk of macaque-human pathogen transmission, unlike findings from Bali, Gibraltar, and Mt. Emei, China. Although infrequent, macaque feeding is most common among human individuals in cars and with human children present. In this research, I aim to build on the research by characterising macaque-human interactions in the MacRitchie Reservoir Park in the Central Catchment Nature Reserve, Singapore, to understand how contexts of human behaviour and macaque life history traits influence the rates and types of human-macaque interactions.

Macaque-human interaction studies have been conducted across the genus, including Barbary macaques (*Macaca sylvanus*) in Gibraltar (O'Leary and Fa, 1993; Fuentes, 2006), rhesus macaques (*Macaca mulatta*) in Hong Kong (Wong and Ni, 2000) and India (Beisner et al., 2015; Balasubramaniam et al., 2020), Tibetan macaques (*Macaca thibetana*) in China (Zhao, 2005; McCarthy et al., 2009), formosan macaques (*Macaca cyclopis*) in Taiwan (Hsu et al., 2009) and bonnet macaques (*Macaca radiata*) in India (Balasubramaniam et al., 2020). Long-tailed macaques (*Macaca* *fascicularis*) have been studied in Singapore (Fuentes, 2008; Sha et al., 2009; Riley et al., 2016), Hong Kong (Wong and Ni, 2000), Malaysia (Balasubramaniam et al., 2020), and Indonesia, in Bali (Wheatley et al., 1994) and West Sumatra (Ilham et al., 2018). Studies have primarily examined the impact of human behaviour on macaque behaviour, specifically in relation to food provisioning by tourists and visitors. Results indicate a positive correlation between the rate of human provisioning activities and the rate of interactions, with higher provisioning leading to more interactions. Newer research has also studied the impact of social factors and demographic differences on the rate of macaque-human interaction (Morrow et al., 2019; Balasubramaniam et al., 2020). Macaques studied included the long-tailed macaques in Malaysia (Balasubramaniam et al., 2020), rhesus macaques in India (Balasubramaniam et al., 2020), bonnet macaques (*Macaca radiata*) (Balasubramaniam et al., 2020), and moor macaques (*Macaca maura*) in Sulawesi, Indonesia (Morrow et al., 2019). Both Morrow et al. (2019) and Balasubramaniam et al. (2020) highlight the need for detailed intragroup analyses to effectively understand and address management and conservation issues pertaining to human-wildlife interactions.

Studies on human-macaque interactions often focus on provisioning and primate aggression (e.g., O'Leary and Fa, 1993; Wheatley et al., 1994; Zhao, 2005; Fuentes, 2006; Hsu et al., 2009; Beisner et al., 2015). Food provisioning increases the rate and duration of macaque aggression (Hsu et al., 2009) with studies highlighting these as problems to be solved. However, few studies equally consider interactions that did not include food provisioning. Since human provisioning positively correlates with human-macaque interaction, with higher provisioning rates resulting in more interactions, lack of provisioning may indicate fewer or no interactions. Studies incorporating macaque activity budgets have shown that human-macaque interactions only comprised a comparably small proportion of their daily activities and behaviour (O'Leary and Fa, 1993; Riley et al., 2016; Ilham et al., 2018; Kaburu et al., 2019). This suggests that researchers may be focused on presenting a skewed view of human-macaque relations by concentrating on negative interactions. A balanced perspective, also encompassing both positive and neutral aspects, could contribute to the preservation of peaceful human-macaque coexistence, thereby achieving conservation and management success. Thus, it is essential to thoroughly describe and characterize all aspects of interactions, not just the negative ones.

2.2.1 Contexts under which interactions occur

The behaviour of wildlife towards humans may vary depending on the context of the encounter. The context serves as a foundation for interpreting observed and recorded behaviours. The context is what may trigger a macaque to behave in a certain way or interact with humans. Sha et al. (2009) categorized interactions into three human-triggered contexts, i.e., contexts that are initiated by humans, including human provisioning, human provocation, and human retaliation. Human food provisioning and human retaliation contexts are usually linked, since human retaliation mostly involved humans reacting to macaques taking or attempting to take their food. Human provocation involves displaying challenging behaviour which may be perceived as aggressive to monkeys, such as pointing, waving, or shouting at them to provoke a reaction, whether humans intend to do so or not (McCarthy et al., 2009).

Studies suggest that most human-macaque interactions are initiated by humans (O’Leary and Fa, 1993; Sabbatini et al., 2005; Hsu et al., 2009), but there can also be contexts without clear human causes, such as in monkey-initiated encounters (O'Leary and Fa, 1993; Sabbatini et al., 2005, and McCarthy et al., 2009; McKinney, 2014). For instance, monkeys may initiate interactions potentially due to associative learning (O’Leary and Fa, 1993). Associative learning is a process whereby monkeys have learned to associate specific objects, people, or actions with certain rewards and outcomes. Monkeys may associate certain humans as non-threatening and initiate interactions with them through proximity, touch, or jumping on them in an affiliative manner (Hsu et al., 2009). Monkeys may also initiate interactions when they feel threatened by human presence, such as protecting their young (Fa, 1992; Beisner et al., 2015). However, in encounters involving high-calorific human food rewards, some interactions that appear monkey-initiated may be considered human-initiated due to associative learning from indirect food provisioning.

2.2.1.1 Direct and indirect provisioning

Food provisioning can cause rapid habituation of wildlife, causing individuals to approach humans for food and potentially behave aggressively towards humans (Morrow et al., 2019). Food provisioning is largely a human-initiated context and can comprise direct or indirect provisioning. Direct provisioning occurs when humans intentionally offer or provide food to wildlife, behaving as a “rewarding human” (Goumas et al., 2020). For instance, humans intentionally contribute to food resources by installing bird feeders and feeding wildlife directly (Civitello et al., 2018). While direct provisioning involves intentionally offering food to wildlife, indirect provisioning occurs when the act is unintentional on the part of the human. For example, through crop planting which wildlife can freely access, forage, and “raid” (Chiyo, Moss and Alberts, 2012; Civitello et al., 2018; Fehlmann et al., 2021).

Research on primate-human interactions since the 1900s shows humans enjoy interacting with and feeding monkeys (e.g., O’Leary and Fa, 1993; Wheattley et al., 1994; Wong and Ni, 2000; Sabbatini et al., 2005; Fuentes and Gamerl, 2005). Direct provisioning may enhance the psychological wellbeing of and economic benefits for both human (monetary) and primates (human food), as demonstrated in India’s Aligarh district and Tughladqabad (Malik, 1988; Southwick and Siddiqi, 1983; Kaburu et al., 2019), the Monkey Forest in Ubud, Bali Indonesia (Wheattley et al., 1994) and West Sumatra (Ilham, 2018), Hong Kong’s Kowloon Hills (Wong and Ni, 2000), and the Parque Nacional de Brasilia in Brazil (Sabbatini et al., 2005) to name a few.

Humans directly provisioning primates has been cited as a popular daily occurrence, particularly during peak tourist seasons in many parts of the world. Often endorsed by governments, food provisioning is a prevalent practice in tourism cultures (Zhao, 2005; Fuentes, 2006; Balasubramaniam, 2020), as seen in the Balinese village of Ubud, where temple staff provide daily provisions to monkeys, and local stakeholders welcome tourists to feed them (Wheatley and Harya, 1994; Fuentes, 2006). In Padangtegal, Bali, despite a prohibition on tourists feeding monkeys, staff only intervened when the monkeys became aggressive (Fuentes, 2006), while people in Gibraltar are known to feed Barbary macaques regularly without facing public fines (Fuentes, 2006).

In addition to direct provisioning, humans may also indirectly contribute to anthropogenic resources by planting crops, fertilizing fields, growing fruit trees in residential properties, putting out food in religious offerings, or disposing of food in unsecured rubbish in urban areas (Shah et al., 2009; Chiyo et al., 2012; Civitello et al., 2017; Fehlmann et al., 2021). Indirect provisioning may also occur when humans accidentally drop food, hold a food carrier which macaques have learned to associate with food, or leave food trash within easy access to monkeys (Sha et al., 2009; Goumas, 2020).

2.2.1.2 Human-initiated interactions and contact

Humans frequently initiate interactions with wildlife and primates due to their preference for close contact with wildlife, often involving direct food provisioning and proximity to wildlife. On interactions between various primate species and humans, humans initiate on average almost four times as many interactions as monkeys (O’Leary and Fa, 1993; Sabbatini et al., 2005; Hsu et al., 2009). Although macaques also initiate interactions with humans, an overwhelming majority of human-primate interactions occur within human-initiated contexts via food provisioning. Human-initiated food-related interactions account for most interactions, with some interactions involving physical contact, as humans give food directly to monkeys (O'Leary and Fa, 1993). Since human provisioning is positively correlated with human-primate interaction, less provisioning could result in fewer interactions. This has been demonstrated in Singapore where provisioning activities are prohibited and enforced with fines leading to fewer provisioning and human-macaque interactions compared with other countries (Fuentes, 2008; Sha et al., 2009; Riley et al., 2016). Restricting provisioning as a mitigating strategy for interface management can reduce problematic interactions involving macaque aggression. Humans often initiate interactions with monkeys based on macaque life history traits. For instance, humans prefer younger monkeys, or mothers with infants (e.g., O’Leary and Fa, 1993; Sabbatini et al., 2005). However, older, sedentary macaques are often easier to interact with due to their tolerance for close contact, while younger macaques are more active and seldom remain still long enough to touch (O’Leary and Fa, 1993; Sabbatini et al., 2005).

2.2.1.3 Proximity / Sharing space

Some scholars have explored wildlife activity budgets, with results suggesting that wildlife may share space in overlaps with humans, e.g., use the same environment and substrates as humans, without significantly spending time in human proximity or interacting with humans. In O'Leary et al.'s study, although the rate of human-macaque interactions was highest during tourism peak time at nearly a hundred interactions per hour, only 13% of macaque activity budget was spent interacting with humans. Similarly, capuchin groups typically live peacefully with humans, with over half of their activity budget occurring in human proximity without human provisioning (Sabbatini et al. 2005). In long-tailed macaques in Singapore, authors found human-macaque interactions accounted for less than 10% of their activity budget, with around 40% of the budget in human proximity without resulting in interactions (Riley et al. 2016). The authors also reveal that due to the low frequency of macaque-human interactions, data on interactions were excluded from the study. These studies suggest that except for human provisioning expectations, monkeys typically spend their time sharing the same space with humans without interacting with them, demonstrating the opportunistic nature of their foraging strategies.

2.2.2 Types of behaviour

Human-macaque interactions can involve affiliative or submissive types of behaviours, as well as aggressive types of behaviour (Kaburu et al., 2019). Aggressive macaque behaviour can include facial threats such as baring of teeth (McCarthy et al., 2009), mobbing, lunging, and chasing, or aggressive contact, including scratching and biting (O'Leary and Fa, 1994; Sha et al., 2009). Displaying aggressive behaviour towards humans can result in aggressive or negative human-macaque interactions. Negative interactions occur when one or both parties experience unpleasant or adverse outcomes from the interaction. For example, a negative interaction can occur when humans retaliate against, or run away from macaque aggression. Affiliative macaque behaviour can include contact or non-contact interest towards humans without the display of any aggressive type of behaviour (Kaburu et al., 2019), leading to neutral or even some positive or affiliative type of interactions (Hsu et al., 2009). Examples can include friendly approaching, touching, or jumping on humans (Hsu et al., 2009).

Many studies focus on negative interactions, particularly involving aggressive macaque behaviour (O'Leary and Fa., 1993; Wheatley and Harya, 1994; Wong and Ni, 2000; Fuentes and Gamerl, 2005;

Fuentes 2008; Hsu et al., 2009; McCarthy at al., 2009; Sha et al., 2009; Lee and Davey, 2015; Ilham et al., 2018). Human provisioning in human-initiated contexts has been studied extensively, with aggressive macaque behaviours and negative interactions being reported as the most common outcome associated with it (O'Leary and Fa., 1993; Wheatley and Harya, 1994; Wong and Ni, 2000; Fuentes and Gamerl, 2005; Fuentes 2008; Hsu et al, 2009; McCarthy, 2009; Sha et al., 2009; Lee and Davey, 2015; Ilham 2018). However, although many negative interactions are due to human provisioning, some occur when humans try to provoke monkeys (McCarthy et al., 2009), or retaliate against monkeys "stealing" food (Sha et al., 2009). Humans may provoke or retaliate by displaying threatening behaviour, such as shouting or waving aggressively (Sha et al., 2009). Macaque aggression can be influenced by aggressive and intimidating human behaviour (Beisner et al., 2015). Human aggression can lead to a reciprocal aggressive response (Hsu et al., 2009; Sha et al., 2009; McCarthy et al, 2009; Beisner et al., 2015; Morrow et al., 2019), or a submissive response, where the monkey flees or displays a submissive grin (Hsu et al., 2009).

Aggressive macaque-to-human interactions often occur in human food provisioning contexts, as macaque aggression is often unintentionally reinforced through being rewarded for aggression towards humans. Most studies show positive correlations between human food availability and aggressive behaviour in macaques (Wheatley and Harya, 1994; Fuentes, 2006) including a high rate of tourists being bitten (Fuentes, 2006). And yet, most macaque behaviours toward humans are affiliative or submissive and aggressive macaque behaviour is less than non-aggressive behaviour. In over half of all interactions comprising human provisioning, agonistic behaviour accounted for only 2.4% of the Barbary macaque's activity budget (O'Leary and Fa, 1993). Although food provisioning resulted in a higher rate and longer bouts of aggression by the Formosan macaques against tourists (Hsu et al., 2009), 90% of human-macaque encounters were peaceful without "conflict". In capuchins, high aggression involving chasing or threatening humans over food is driven by only a few individuals (Sabbatini et al. 2005), indicating this behaviour is unusual among the population.

Future studies could usefully examine and highlight the types of behaviour or interactions beyond the negative. Research could include more analyses and discussions regarding affiliative human and macaque behaviours, as well as when humans and macaques maintain neutrality, ignoring each other during encounters (e.g., Sha et al., 2009, Hsu et al., 2009; Kaburu et al., 2019). This is important, since monkeys not reacting to the presence of humans may demonstrate that they are treating humans merely as an inconsequential factor of their environment, not dissimilar to how most wildlife may view humans (Goumas, 2020). More relevant to my study, it may be possible to demonstrate that the co-occurrence of humans and wildlife is not always a problematic situation requiring interventions (e.g., Sha et al., 2009; Riley et al., 2016).

2.3 How different life history stages influence human-primate interactions

Factors influencing learning and behaviour in social wild animals are crucial for understanding their response to changing environments and conservation (Chiyo et al., 2012). These factors are relevant for understanding the prevalence of behaviours such as foraging on cultivated crops or livestock, leading to challenging human-wildlife interactions and human or wildlife mortality in human-controlled environments (Chiyo et al., 2012). Understanding the likelihood of certain individuals initiating interactions with humans, engaging in long interactions, and resorting to costly behaviours like aggression can aid in reducing problematic interactions and promoting peaceful coexistence (Balasubramaniam et al., 2020).

Both intrinsic wild animal characteristics and extrinsic socioecological factors can influence wildlife behaviour in anthropogenic landscapes (Balasubramaniam, 2020). Intrinsic characteristics can influence wildlife interactions with humans that are related to life history, such as sex and age (Fuentes 2005; Hsu et al., 2009; Chiyo 2012; Morrow 2019). As individual energetic demands are linked to these life-history traits, some animals may engage in riskier behaviours than others, such as risking human retaliation in obtaining human food (Wolf 2007; Morrow 2019). Life history theory suggests age-sex differences in risk-taking behaviour, due to different fitness expectations and energetic requirements, may be visible in anthropogenic contexts through intraspecific differences in human interaction and resource exploitation (Ross, 1992;Janson and van Schaik, 2002; Wolf et al., 2007; Chiyo, 2012; Morrow et al., 2019). Some individuals may prioritize future fitness returns over others due to the trade-offs between current and future reproduction (Clark, 1987; Roff, 2002; Rueffler et al., 2004; Wolf, 2009).

According to earlier studies, male animals tend to forage in agricultural land and urban garbage, and have greater access to anthropogenic food than females, as seen in African elephants (Chiyo et al., 2012), black bears (Lischka et al., 2018), and primate species such as baboons (Fehlmann et al., 2017), capuchins (Sabbatini et al., 2015) and macaques (Morrow et al., 2019; Balasubramaniam et al., 2020). Males face high energetic demands to retain physical features such as larger horns, and body sizes which increase their competitive edge and reproductive success (Mitani, Gros-Louis and Richards, 1996; Clutton-Brock, 2017). Although primates such as the macaques are not obviously sexually dimorphic, they have strict dominance hierarchies. High-ranking individuals, specifically males, tend to have better reproductive success and quality of offspring, but acquiring and maintaining dominance may require significant energetic costs due to greater agonistic and sexual activities (Gesquire et al., 2011).

Thus, due to life-history traits, male primates are more likely to take risks to obtain high-energy human foods while females may be more risk-averse due to high reproduction costs and greater potential for loss (Clark, 1987; Roff, 2002; Rueffler et al., 2004; Wolf, 2009; Morrow et al., 2019; Balasubramaniam et al., 2020). Adult males may be more risk-prone than non-adult males due to high reproductive potential, competition for mates, and lower risk of mortality due to their larger body sizes (Gesquire et al., 2011; Morrow et al., 2019). Peripheralized sub-adult males (Morrow et al., 2019) may exhibit increased risk-taking behaviour due to dispersal from natal groups (Chiyo et al., 2012), avoiding male-male competition, and avoiding inbreeding (Lute, Hollocher and Fuentes, 2014). Further, juveniles across the sex class may be more risk-averse due to higher mortality risks due to smaller body size compared to older, larger-sized primates (Dunbar, 1987; Promislow and Harvey, 1990; Janson and van Schaik, 2002). However, regardless of age, some macaque species, e.g., male moor macaques, engage more in human interactions than female macaques (Morrow et al., 2019). This may be because males in wildlife species may also be more likely to take risks due to their exploratory behaviour and bold personality (Morrow et al., 2019; Balasubramaniam et al., 2020). In support of this argument, male macaques, including long-tailed macaques and Formosan macaques, exhibit more frequent and aggressive interactions with people than female macaques

(Fuentes and Gamerl, 2005; Hsu et al., 2009; Balasubramaniam et al., 2020). However, female macaques may also exhibit increased aggression and reliance on anthropogenic food when rearing offspring, due to the need to protect their offspring and meet the energetic demands of offspring rearing (Fa, 1992; Beisner et al., 2015).

Life history traits may influence human behaviour towards primates and whether primates are more or less likely to behave with aggression towards humans. For example, while older monkeys initiate more food-related interactions with humans than younger monkeys, due to human preference for interacting with infants and juveniles, these sex/age groups were the most observed group interacting with humans, with high rates recorded for mothers and infant monkeys (O'Leary and Fa, 1993; Sabbatini et al., 2005). Humans tend to favour adult female monkeys with infants as provisioning targets (O'Leary and Fa, 1993) and younger cuter monkeys (Sabbatini et al., 2005), leading to lower aggression in these animals as they do not have to display aggressive behaviours to obtain human food (O'Leary and Fa, 1993; Fuentes and Gamerl, 2005). In snub-nosed monkeys (Rhinopithecus *bieti*) immature individuals tend to exhibit more affiliative behaviours towards humans, while adult males tend to exhibit more aggressive behaviours towards humans (Xia, Hu and Krzton, 2017). Male primates, who are less provisioned by humans than females with infants, or juveniles, may exhibit increased inter-species aggression and intra-group aggression, particularly towards their subordinates (O'Leary and Fa, 1994; Fuentes and Gamerl, 2005). Thus, aggression in macaque-to-human interactions may be higher among adult and sub-adult male macaques than females and juveniles, due to life history traits influencing human behaviour.

According to Balasubramaniam et al. (2020), social characteristics in primates, such as dominance rank and network connectedness, can influence their resource access, and risk-taking tendencies, linked to their life history traits. Although these are beyond the scope of this study, it may be possible to draw some inferences by comparing studies, such as with Morrow et al.'s 2019 research investigating how life history and social network factors influence interindividual variation in human-primate interactions. In Balasubramaniam et al.'s study (2020) which examines the impact of animals' life-history and social attributes, spatially peripheral individuals interact most with humans. According to Morrow et al. (2019), these individuals tend to be less centrally connected sub-adult males. Higher-ranking individuals also initiate more interactions, which tend to be adult males, particularly older males (Morrow et al., 2019), while individuals incurring lower reproduction costs due to their life history and resource access, i.e., adult, and sub-adult males, are more likely to take risks in anthropogenic environments (Morrow et al., 2019; Balasubramaniam et al., 2020).

2.4 The human-macaque interface in urban Singapore

Singapore, a land-scarce island city state of 721.5 km2 (Li et al., 2021) and home to 5.6 million people (Ngo, Hosaka and Numata, 2019), has claimed most of its forest cover for industrialization and urbanization (Li et al., 2021). Main forest reserves remain in Bukit Timah, Central Catchment Nature Reserves, and military training areas, which is a series of forest reserves and reservoirs in Singapore's central region (Sha et al., 2009; Li et al., 2021). There are limited buffer zones between reserve patches and human habitations, although smaller forest patches in the military training area are typically state-protected areas with restricted public access (Li et al., 2021).

Singapore is renowned for its frequent human-wildlife interactions, as its urban residences are built within the natural range of wildlife, including macaques (Fuentes, 2008). Media reports reveal that mammalian wildlife have become more frequently encountered at human-wildlife interfaces such as wild boars (*Sus scrofa*) and sea otters (*Enhydra lutris*), and primates including long-tailed macaques and the critically endangered Raffles' banded langurs (*Presbytis femoralis*) (Owa et al., 2022). Singapore is also home to a third primate species, the Sunda slow loris (*Nycticebus coucang*) (Ang et al., 2021), but the most common primate species here are the long-tailed macaques (Li et al., 2021). Long-tailed macaques are found primarily in local forest patches, with around 70% of its 1900 population residing in the Bukit Timah and Central Catchment Nature Reserve (Sha et al., 2009; Riley et al., 2015b; 2016; Li et al., 2021). The long-tailed macaque population is predicted to rise by 25% by 2030, which is expected to increase human-macaque encounters leading to interactions (Riley et al., 2016).

Singapore's human-primate interface is relatively mild compared to other countries where high rates of human-primate interactions occur through monkey feeding by tourists, pilgrims, and locals (O'Leary and Fa, 1993; Wheatley and Harya, 1994; Zhai, 2005; Fuentes et al. 2008; Sabbatini et al., 2009; Ilham et al., 2018; Morrow et al., 2019; Balasubramaniam et al., 2020). Humans directly provisioning primates involving physical contact have been cited as a popular daily occurrence in other countries. Food provisioning is particularly prevalent in tourism cultures as they are often endorsed by governments (Zhao, 2005; Fuentes, 2006; Balasubramaniam, 2020). Whereas in Singapore, human-macaque interaction and direct physical contact is low (Fuentes et al., 2008; Sha et al., 2009). For instance, Singapore's human-macaque interactions are only two percent of Gibraltar's high rate of nearly 100 interactions per hour (O'Leary and Fa, 1993; Sha et al., 2009). Macaques in Singapore also spend less than 10% of their activity budget interacting with humans (Riley et al., 2016). Despite this, Singapore's newspaper reports reveal a persistent lack of tolerance towards macaques, with media headlines presenting public perception of macaques more negatively than positively (Sha et al., 2009). There may be a few reasons for this.

In highly urbanized Singapore, residents often perceive wildlife negatively and fear them due to limited wildlife knowledge and exposure (Ngo, Hosaka and Numata, 2021). This is because Singaporeans are less likely to have grown up in nature than people from developing countries (Ngo et al., 2019). However, the low rate of human-macaque interaction may also be due to the non-marketing of monkeys as visitors' attractions, and strict government regulations against feeding macaques (Fuentes et al., 2008; Sha et al., 2009). It is a criminal offense to feed wildlife, punishable by a fine of up to S$50,000, a six-month jail term, or both (Tan, 2016). As revealed in other countries, humans are also a root cause of problematic human-macaque relations in Singapore (Wong, 2017; Iau, 2019).

In Singapore macaques mostly interact with humans along roadsides and urbanized recreation parks on forest fringes (Sha et al., 2009; Riley et al., 2016). However, rapid urbanization and land use changes in Singapore have led to increased proximity and interaction between long-tailed macaques and the general human population (Li et al., 2021). As residential development encroaches on macaques' natural habitats, damaging crucial wildlife corridors (Li et al., 2021), macaques are more frequently seen outside forest fringes in urban areas, foraging on human garbage, entering homes, and receiving direct provisioning from humans (Tan, 2016). Further, although the number of people directly feeding monkeys has decreased significantly, it has not stopped completely (Iau, 2019). The provisioning of macaques in Singapore despite the feeding ban has continued to lead to an increase in problematic human-macaque interactions and public complaints, as only some humans feed monkeys, but not all, specifically those who make the complaints. This is a case of human-human conflict as previously discussed.

The media reports high rates of complaints against macaque aggression towards humans, such as monkeys chasing people and entering people's homes (Feng, 2015; Tan, 2016). Singapore's government had previously attempted to control macaque populations by culling to address human-macaque overlaps and public complaints (Lee and Chan, 2011; Riley et al., 2016), but conservation groups and academics argue culling is not sustainable, with survey results showing most residents oppose culling and favour education (Zheng, 2015). Consequently, the government, and its agencies, such as NPark (National Parks Board, 2023), various academics and ACRES (the Animal Concerns Research Education Society), have implemented newer measures to address the issues, such as increasing public education campaigns on avoiding interactions with macaques, issuing stricter fines for feeding wildlife, and conducting monkey guarding, involving blocking monkeys on park corridors and herding them towards the forests away from residential areas (Tan, 2017; Thong, 2017; How, 2020).

Studies on Singapore macaques have mainly highlighted the negative impacts of human provisioning leading to problematic human-macaque relations (e.g., Fuentes, 2008; Sha et al., 2009 and Riley et al., 2016). Most interactions occur in human-initiated contexts involving food provisioning and macaque aggression, which is prevalent in other research. Singapore studies also highlight human-macaque conflict, focusing on the need to mitigate these with limited discussion on positive human-macaque relations (e.g., Fuentes, 2008; Sha et al., 2009). This unbalanced focus may be due to the field's emphasis on management issues requiring knowledge of social science and often funded by agencies experiencing these issues, but it also reinforces negativity bias (Buijs and Jacobs, 2021).

To ensure sustainable coexistence for humans and wildlife, reduce human fear of wildlife and increase their knowledge of the benefits of coexistence (Buijs and Jacobs, 2019), research could focus on all interactions, including positive and neutral ones. Coexistence ensures wildlife population longevity while managing tolerable human risks (Carter and Linnell, 2016; Frank, 2016; Mekonen, 2020; Pooley et al., 2020; Konig et al., 2021). Research aiming for balanced understanding of human-macaque interactions and positive psychology (Buijs and Jacobs, 2019) will provide descriptions of all behaviours and interactions, including no interactions. This will foster positive relations between humans and primates in interfaces and ultimately boost conservation success (Frank, 2016; Mekonen, 2020; Konig et al., 2021).

Chapter 3

Research questions, hypotheses, and predictions

In this research, I aim to characterise macaque-human interactions within a nature park in Singapore, then examine how human behaviour and macaque life history traits influence the rates and types of interactions that occur. To achieve this, I will analyse quantitative behavioural data of both macaques and humans observed during encounters in Singapore. Encounters will occur when humans and macaques are within an approximately three-metre distance of each other, which may or may not result in an interaction.

I will first ask the question in what context will macaques interact with humans more and what are the types of interactions. To establish the context in which macaques interact with humans at a higher rate and the types of interactions, I followed Sha et al.'s (2009) protocol for documenting contexts initiated by humans, i.e., (1) human feeding contexts, (2) human provocation contexts, and (3) human retaliation contexts, and will group them under the category "human-initiated contexts". Human-initiated contexts refer to any context of interaction caused by human behaviour, activity or actions in macaque proximity, including indirect provisioning. I will also add a fourth category, (4) "human-neutral contexts", which refers to situations where no human causes for macaque behaviour or macaque-to-human interactions are observed, except for being in macaque proximity. Under this category, interactions observed may also have been initiated by macaques (O'Leary and Fa, 1993; Hsu et al., 2009; McCarthy et al., 2009). I will also consider three types of macaque behaviour towards humans to document macaque-to-human interactions, including (1) aggressive, (2) affiliative, and (3) submissive behaviours (Sha et al., 2009).

Further, I will also be asking whether interactions with humans differ between macaque demographic categories. To my knowledge, research has not yet been done in Singapore on demographic differences influencing interactions based on life history traits. According to life history theory, adult male macaques may be more likely to take risks and interact with humans than risk-averse female (Morrow et al., 2019) and juvenile macaques (Janson and van Schaik, 2002). Sub-adult males, who often live on the periphery before dispersing to join or form new groups, have also been found to interact more with humans than females, or juveniles (Balasubramaniam et al., 2020). However, life history traits may influence human behaviour to reverse this trend, for example, by humans preferring to interact with, and provision, adult female macaques with infants and juvenile macaques. The competition over human food may increase aggression among males (adult and sub-adult), leading to more aggressive behaviour against humans by these group categories than females and juveniles.

Research question 1:

In what context will macaques interact with humans at a higher rate and what are the types of interactions?

I hypothesise that the context of an encounter will influence the rate and type of macaque-human interactions. I predict that in human-initiated contexts:

1. Macaques will interact with humans more than in human-neutral contexts, as human-neutral contexts lack human food involvement.
2. Interactions with humans will be more aggressive than affiliative or submissive in human feeding contexts, as studies have suggested that macaque aggression is positively correlated with human feeding.

3. Interactions with humans will be more affiliative or submissive than aggressive in human provocation contexts, as humans may either accidentally or purposely provoke a reaction from monkeys, e.g., by pointing or advancing too close to monkeys causing monkeys to flee.
4. Interactions with humans will be more affiliative or submissive than aggressive in human retaliation contexts, as humans often use aggression or shouting to prevent monkeys from obtaining their food.

I also predict that in human-neutral contexts:

5. Interactions with humans will be more affiliative or submissive than aggressive, as human-neutral contexts lack human food involvement.

Research question 2:

Will interactions with humans differ between macaque demographic categories?

I hypothesise that interactions with humans will differ between macaque demographic categories. As females and juveniles are expected to be more risk-averse than adult and sub-adult male macaques, I predict that in both human-initiated contexts and human-neutral contexts:

1. Adult and sub-adult males will interact with humans more than females or juveniles.
2. There will be more aggressive interactions with humans among adult and sub-adult males than among females and juveniles.
3. There will be more affiliative or submissive interactions with humans among females and juveniles than among adult and sub-adult males.

Chapter 4

Methods

4.1 Study site and subjects

To characterise human-macaque interactions during encounters, I analysed and obtained behavioural data from field observational video recordings of two groups of wild long-tailed macaques residing at the Singapore MacRitchie Reservoir Park within the Central Catchment Nature Reserve (see Figure 1 for a map of MacRitchie Reservoir Park). The park, surrounded by residential properties, is a popular destination for various human users, including wildlife watchers, sports enthusiasts, hikers, and day-trippers, making it an ideal interface zone for macaque-human interaction studies (Sha et al., 2009). Human-macaque encounters can often be observed in shared spaces like forest trails, boardwalks and paved footpaths, an outdoor gym, the Alfresco-style Mushroom Café, and a local bus stop. MacRitchie Park was a site in earlier research that investigated numerous resident complaints against macaques (see Figure 1b), perceivably due to the high macaque population living there (Sha et al., 2009). About 70% of the macaque's 1900 population reside in the Central Catchment Nature Reserve (Sha et al., 2009; Riley et al., 2015b; 2016). Thus, a follow-up study of macaques at this location is appropriate and timely for exploring the status quo of macaque-human interactions (e.g., Sha et al., 2009 and Riley et al., 2016).

The field videos were recorded by field assistant Simpson between July 14th and September 29th, 2019, comprising 1729 two-minute focal sample recordings of 51 macaque individuals combined, totaling around 58 hours of recorded video data. Macaque individuals were already preidentified and sex/age-classed by Simpson (see Table 1 for a list of the study subjects). Simpson worked six days a week, alternating group follows daily. The two macaque groups were chosen for recording due to the park being located within the macaques' home range, including areas that are heavily frequented by visitors. Videos were recorded using a Sony Cyber-shot DSC HX400V Digital Camera, and 1249 images were taken for individual identification (Simpson, 2021). Macaque age and sex classification was assessed based on individual body size, fur colouring, genitalia type (Morrow et al., 2019), and sexual organ developmental stage (Sha, 2013). Males were classified as adults if they had fully developed secondary sexual characteristics, such as large, descended testes and well-developed musculature, while some sub-adult males typically might have slimmer musculature. Fully grown females showed evidence of parity (elongated nipples from lactation), juveniles had full adult coloration without sexual maturity, and infants had no sexual maturity and black fur (Fooden, 1995; Mittermeier and Nash, 2013; Riley, Jayasri and Gumert, 2015). Altogether the dataset included 20 adults (six males), 13 sub-adults (seven males), and 20 juveniles (10 males). Simpson also recorded four infants, but as the mothers mostly carried them, the infants were excluded from this study's dataset.

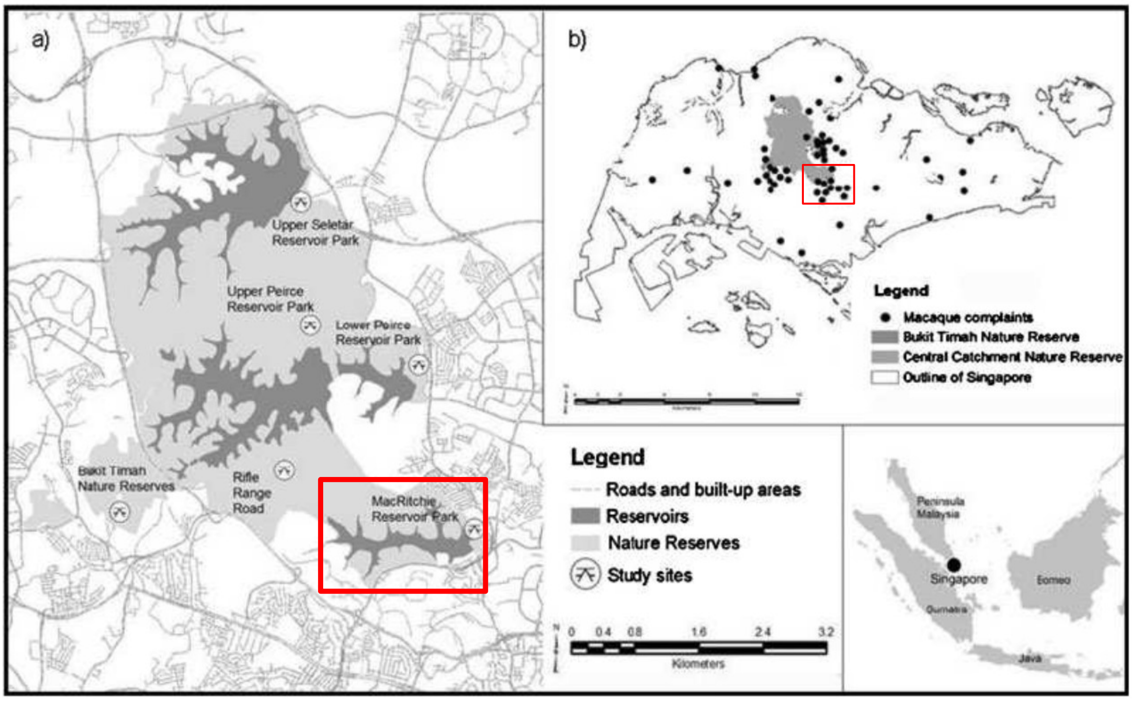

Figure 1: a) A map for MacRitchie Reservoir Park location (highlighted in red), one of several sites

studied in previous research; b) sites investigating resident complaints against macaques (Sha et al., 2009).

Table 1: A list with sample numbers and sample times of the 51 study subjects comprising 35 individuals from CG and 16 individuals from ZZ.

No	Group	Id	Sex	Age	Sample number	Sample time in minutes
1	CG	ANG	F	Adult	30	60
2	CG	BEC	F	Adult	32	64
3	CG	DOL	F	Adult	27	54
4	CG	DUC	F	Adult	24	48
5	CG	ELS	F	Adult	27	54
6	CG	JOL	F	Adult	34	68
7	CG	MEG	F	Adult	28	56
8	CG	REG	F	Adult	29	58
9	CG	BOR	M	Adult	30	60
10	CG	FRA	M	Adult	34	70
11	CG	JUL	M	Adult	38	78
12	CG	KNO	M	Adult	32	64
13	CG	DUK	F	Subadult	30	60
14	CG	JES	F	Subadult	33	66
15	CG	LIV	F	Subadult	27	54
16	CG	LIZ	F	Subadult	30	60
17	CG	MOR	F	Subadult	26	52
18	CG	JAM	M	Subadult	38	76
19	CG	LIO	M	Subadult	29	58
20	CG	LUI	M	Subadult	22	44
21	CG	MAR	M	Subadult	34	68
22	CG	BAT	F	Juvenile	33	66
23	CG	BEE	F	Juvenile	27	54
24	CG	CHL	F	Juvenile	31	62
25	CG	CLA	F	Juvenile	21	42
26	CG	HAY	F	Juvenile	25	50
27	CG	AND	M	Juvenile	23	46
28	CG	BRU	M	Juvenile	24	48
29	CG	ERI	M	Juvenile	25	50
30	CG	FLU	M	Juvenile	27	54
31	CG	KEN	M	Juvenile	25	50
32	CG	LOV	M	Juvenile	21	42

33	CG	ROB	M	Juvenile	34	68
34	CG	TIM	M	Juvenile	28	56
35	CG	VIL	M	Juvenile	26	52
36	ZZ	CHI	F	Adult	38	76
37	ZZ	FIG	F	Adult	53	106
38	ZZ	JUA	F	Adult	62	122
39	ZZ	MAB	F	Adult	45	90
40	ZZ	TER	F	Adult	57	114
41	ZZ	BON	M	Adult	57	114
42	ZZ	PAU	M	Adult	12	24
43	ZZ	TAY	F	Subadult	52	104
44	ZZ	ELT	M	Subadult	25	50
45	ZZ	MIL	M	Subadult	51	102
46	ZZ	TIP	M	Subadult	59	118
47	ZZ	ASA	F	Juvenile	31	62
48	ZZ	COC	F	Juvenile	45	90
49	ZZ	FER	F	Juvenile	35	70
50	ZZ	FRO	F	Juvenile	51	102
51	ZZ	KOR	F	Juvenile	53	106

4.1 Data collection

Simpson followed sampling protocol to video-record each focal follow, using a randomiser to decide on the order at which individuals were sampled thereby minimizing sampling bias. Simpson also recorded and narrated contextual information over each video recording, including date, time, location, and human proximity in human-macaque encounters, as well as off-camera information, e.g., on humans who were unseen. From these focal follows, I conducted all occurrences sampling (Altmann, 1974) to obtain data on human and macaque behaviour. All occurrence sampling allows for accurate recording of short discrete events and behavioural frequencies (Martin and Bateson, 2007). I also made ad libitum observations of focal behaviours during and outside human encounters, including resting, traveling, socialising and foraging, both alone and with conspecifics.

Encounters occurred when humans and macaques are within an approximately three-metre distance of each other, which may or may not result in an interaction. From each encounter, I sampled behavioural and interaction data for both humans and macaques as defined by the rules of an ethogram I created in

BORIS for Windows 10 (see Table 2 - Ethogram). BORIS (Behavioural Observation Research Interactive Software) is an open-source event coding software for live and video observations developed by Friard and Gamba (2016). It allows the creation and sharing of standardized input and output formats for project-related information, including observations, subjects' lists, ethograms, and variables (Friard and Gamba, 2016). BORIS enabled me to create a subject list and an ethogram of behaviours appropriate for the study.

All behaviours observed in macaques during human-macaque encounters were sampled to obtain descriptive statistics, including aggressive, affiliative, and submissive behaviours, contexts of behaviours, as well as interaction and non-interaction behaviours, i.e., ignoring human. I recorded whether macaques ignored humans or interacted with humans, and if an interaction occurred what behaviour was displayed. I also collected human behaviour data to obtain descriptive statistics for the type of human behaviour as well as catalogue the contexts of encounters and interactions (see Table 2 – Ethogram, for definitions on human and macaque behaviour and contexts). Humans were considered to be present when they were visible on the focal video, heard but not visible, or commented upon by Simpson (e.g., in conversation) to be within three-metre proximity, even if not visible or audible. Although humans ignoring macaques are considered as ‘no interaction’, it is relevant for recording the contexts of the encounters and interaction. To analyse the type and rate of macaque behaviour towards humans based on contexts and demographic differences for inferential statistical analyses, only macaque behaviours were included.

Table 2: Ethogram for coding behaviours during human-macaque encounters when within approximately three metres of each other.

Row/Column	**1**	**2**	**3**	**4**
a)	**Behaviour**	**Definition**	**Interaction type**	**Adapted from:**
Human behaviour in encounters	Appreciating monkey	Human is observed sitting, standing, or slowing down during a walk with clear orientation towards monkey, to observe or photograph monkey	Affiliative	Sha, 2009; Kaburu, 2019
	Avoiding monkey	Human is observed moving away from monkey, e.g., walking around or running from monkey, having registered its presence	Submissive	Sha, 2009; Kaburu, 2019

Hiding food from monkey	Human is observed putting food or drink away in a bag in response to monkey's approach, e.g., to hide food from monkey	Submissive	Sha, 2009
Ignoring monkey	Human is observed not reacting to monkey's presence except for brief glances (e.g., walking, or jogging past)	No interaction	Sha, 2009; Kaburu, 2019
Provisioning monkey	Human is observed giving food or drink to monkey, i.e., direct provisioning, or with feeding cues, i.e., indirect provisioning, e.g., carrying a plastic bag	Affiliative	Sha, 2009; Kaburu, 2019
Challenging monkey	Human is observed advancing closer towards monkey (e.g., to within an arm's length of monkey), whether to appreciate, wave, point, taunt, verbalise loudly, or laugh at monkey	Aggressive	Sha, 2009; McCarthy, 2009; Kaburu, 2019
Threatening monkey	Human is observed chasing, yelling, waving a stick at monkey, or dragging a chair grating the ground, to deter monkey from taking human food or belonging	Aggressive	Sha, 2009; Kaburu, 2019

b)

Macaque behaviour in encounters

Behaviour	**Definition**	**Interaction type**	**Adapted from:**
Ignoring human	Monkey is observed not reacting to human presence except for brief glances	No interaction	Sha, 2009; Kaburu, 2019
Non-aggressive contact	Monkey is observed non-aggressively touching human or human belongings (e.g., bags)	Affiliative	Sha, 2009; Hsu, 2009; Kaburu, 2019
Non-aggressive interest	Monkey is observed looking at or moving towards human without aggressive display (e.g., lip smacking)	Affiliative	Sha, 2009; Kaburu, 2019
Submission	Monkey is observed moving away, running from human, or displaying fear/submissive grin towards human	Submissive	Sha, 2009; Kaburu, 2019
Aggressive contact	Monkey is observed scratching, hitting, or biting human	Aggressive	Sha, 2009; Kaburu, 2019
Grabbing	Monkey is observed taking or attempting to take food or belonging from human	Aggressive	Sha, 2009; Kaburu, 2019
Lunging/chasing	Monkey is observed advancing with speed at human, usually while displaying a visual or vocal threat	Aggressive	Sha, 2009; Kaburu, 2019
Mobbing	Monkey is observed advancing at speed towards, taking or attempting to take food from human with at least another conspecific	Aggressive	Sha, 2009; Kaburu, 2019
Threatening	Monkey is observed making visual (eyebrow raises, piloerection, open-mouth gape, baring teeth) or vocal (grunt hoots) threat displays at human	Aggressive	Sha, 2009; McCarthy, 2009; Kaburu, 2019

c)

Context of behaviour or interaction

Context	**Definition**	**Context type**	**Adapted from:**
Human feeding	When human is observed "Provisioning monkey," carrying feeding cues, e.g., plastic bag, or just eating and ignoring monkey e.g., at the Mushroom Café, etc., and monkey was present. Includes both direct and indirect provisioning.	Human-initiated	O' Leary and Fa, 1993; Sha, 2009; Kaburu, 2019
Human provocation	When human is observed "Challenging monkey" (see **Table 2a**)	Human-initiated	Sha, 2009; Kaburu, 2019
Human retaliation	When human is observed "Threatening monkey" (see **Table 2a**)	Human-initiated	Sha, 2009; Kaburu, 2019
Human-neutral	When human is observed doing nothing to elicit macaque response, except for being near monkey. E.g., human may be ignoring, appreciating, or avoiding monkey. May also include macaque-initiated interaction	Human-neutral	O'Leary, 1993; Sha, 2009; Kaburu, 2019

4.2 Data analysis

I exported data coded and processed in BORIS into Microsoft Excel detailing all events of coded behaviour for each focal individual. All statistical analyses were conducted using SPSS (Statistical Package for the Social Science) Version 26 for Windows. For descriptive statistics, I first presented and analysed the overall data by calculating total counts of each behaviour, types of behaviour and contexts of encounters and interactions using percentages. I then presented inferential statistics by calculating the rate of behaviour or interaction for each focal individual. Analysing frequency counts without including the time observed should be avoided when analysing and measuring behaviour (Merbitz, Merbitz and Pennypacker, 2016). Thus, I calculated hourly rates of focal time by dividing the total frequency count of a behaviour in an encounter by the total recorded minutes for the encounter, multiplied by 60 minutes (Rate = frequency count/recorded minutes*60). For the overall mean rate, I divided the sum of the rate of all behaviours in encounters by the 51 total individuals (sum of rate/51). I then exported the data into SPSS and analysed the rate of behaviours and interactions in SPSS according to the contexts, demographic groups, and types of interactions. I used Mann-Whitney U tests to test for differences in the rate of macaque-to-human interactions across the contexts and the type of interaction to address research question 1, predictions 1–5, as the assumptions for parametric statistics were not being met. To test for differences in the rates of macaque-to-human interaction by sex/age class across the contexts to answer research question 2, predictions 1-3, I used a One Way Anova with Bonferroni corrections. The analyses were then visually presented with charts produced in Excel and SPSS, and tables created in Microsoft Word.

4.3 Ethical considerations

Live animal and human behavioural research require ethical approvals from government and non-governmental bodies such as Durham University's Animal Welfare Ethical Review Board (AWERB) and the Department of Anthropology's Research Ethics and Data Protection Committee. I received ethical clearance from the Research Ethics Committee as my study was a no-contact, non-invasive research using pre-recorded video footages with prior AWERB approval (reference number ANTH-2021-03-25T16_08_09-pfcp95) and no humans were personally identified in the videos. Further, in procuring the field recordings in Singapore, field assistant Simpson I. adhered to NParks' rule of maintaining two-metre social distance, avoiding touching, holding, or abusing animal, taking no selfies, and reporting animal injuries to ACRES, an animal welfare group (Simpson, 2021).

Chapter 5

Results

I studied 3,460 minutes of recordings across 51 focal follows and recorded 2,703 human-macaque encounters. 84.54% (N = 2,285) of the encounters occurred in human-neutral contexts (Figure 2). In total across the contexts, 16.83% (N = 455) of macaque-human encounters resulted in a macaque-to-human interaction (Figure 3). Of these interactions, 52.31% of macaque-to-human interactions (N = 238) were recorded in human feeding contexts (Figure 4). The most common human behaviour was to ignore the monkeys, followed by appreciating them (Figure 5). Generally, the macaques interacted with humans at a mean rate (hereafter "rate") of 7.35 times (±SD 7.45) per focal hour. The overall rate of affiliative or submissive macaque-to-human interactions was 6.84 (±SD 6.96) per hour, while the overall rate of aggressive macaque-to-human interactions was 0.51 (±SD 0.90) per hour (Table 3). See Appendix A for descriptive statistics for each focal individual.

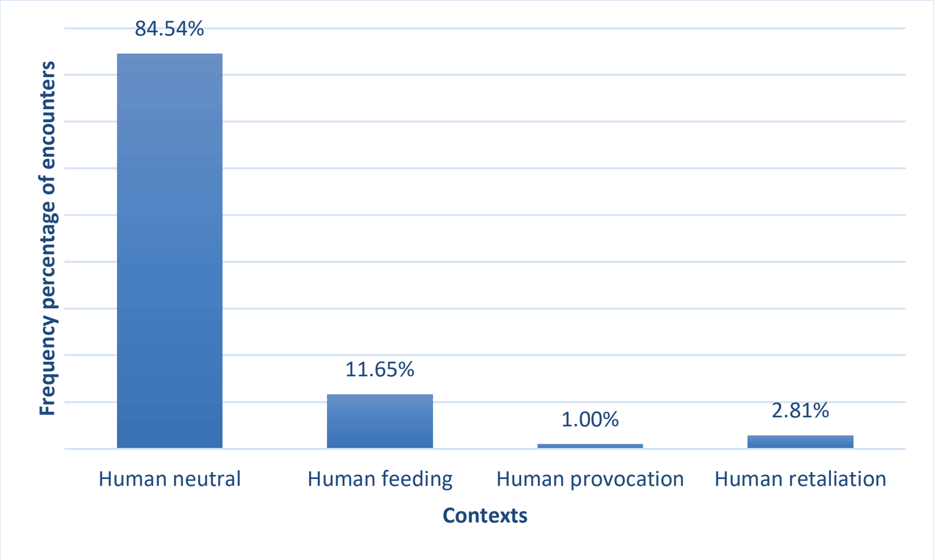

Figure 2: Percentage breakdown of all macaque-human encounters by context. An encounter occurs when macaques and humans are observed within an approximately three-metre distance of each other that may or may not lead to an interaction. Human-initiated contexts included human feeding, human provocation, and human retaliation, while human-neutral contexts included encounters where no human causes for the macaque behaviour were observed, apart from being in proximity to humans.

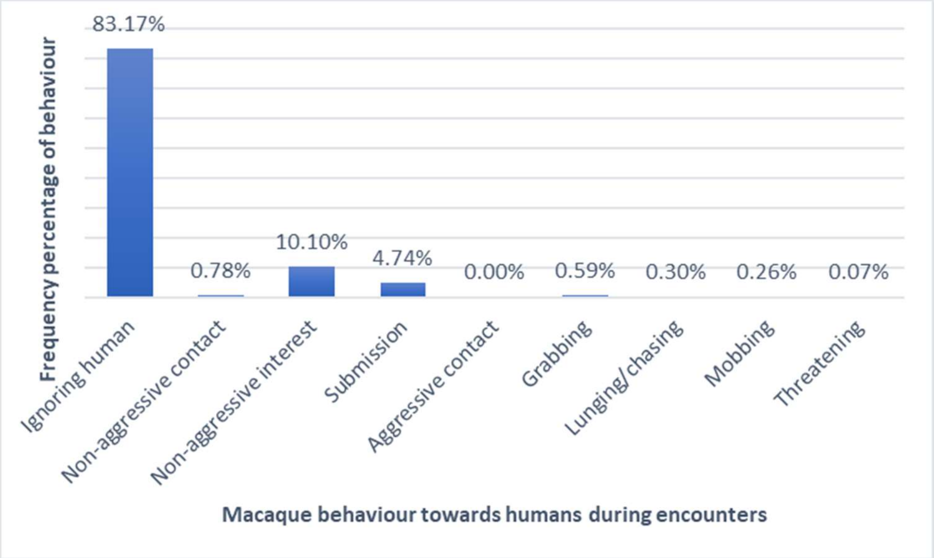

Figure 3: Percentage breakdown of all macaque behaviours during encounters with humans across all contexts.

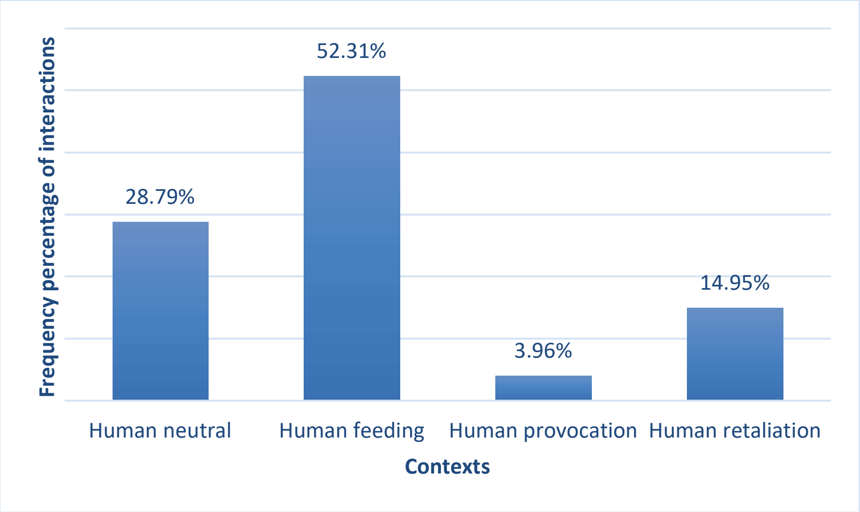

Figure 4: Percentage breakdown of macaque-to-human interactions across the contexts. Human feeding, human provocation and human retaliation are all classed as human-initiated contexts, while human neutral contexts are contexts for which humans did not initiate an interaction, except for being in proximity of macaques.

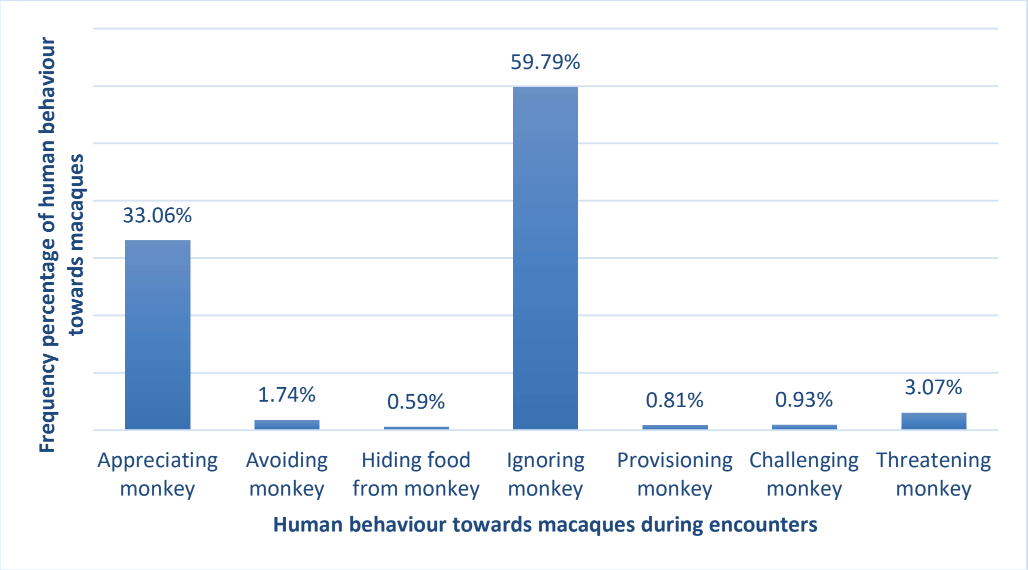

Figure 5: Percentage breakdown of all human behaviours during encounters with macaques across all contexts.

Table 3: Mean (±SD) rate per focal hour of macaque-to-human interaction type across contexts.

Interaction type	All contexts	Human neutral contexts	Human initiated contexts	Human feeding contexts	Human provocation contexts	Human retaliation contexts
All	7.35 (7.45)	2.28 (2.31)	5.07 (5.14)			
Aggressive	0.51 (0.90)	0.01 (0.07)	0.50 (0.83)	0.42 (0.77)	0.00 (0.00)	0.08 (0.33)
Affiliative / submissive	6.84 (6.96)	2.27 (2.31)	4.57 (4.65)	3.34 (3.84)	0.31 (0.57)	0.92 (1.29)

All contexts = Human-neutral + Human-initiated contexts.
Human-initiated contexts = Human feeding + Human provocation + Human retaliation contexts.

5.1 In what context do macaques interact with humans at a higher rate and what are the types of interactions?

5.1.1 Rate of macaque-to-human interactions in human-neutral vs. human-initiated contexts

I predicted that macaques would interact with humans at a higher rate during human-initiated contexts than during human-neutral contexts. Consistent with the prediction, the rate of interactions occurring in human-initiated contexts (mean rank = 59.57) was significantly higher than in human-neutral contexts (mean rank = 43.43) (U = 1712.0, n_1=51, n_2=51, P = 0.006).

5.1.2 Rate of interactions during human feeding contexts and the type of interactions

I predicted that during human feeding contexts, aggressive macaque-to-human interactions would be observed at a higher rate than macaque affiliative/submissive interactions. Contrary to the prediction, the rate of aggressive interactions (mean rank = 36.95) in human feeding contexts was significantly lower than the rate of affiliative or submissive interactions (mean rank = 66.05) (U = 558.5, n1=51, n2=51, P = 0.001). Only 8.89% of macaque interactions with humans (N = 28) involved aggressive macaque behaviour (Figure 6).

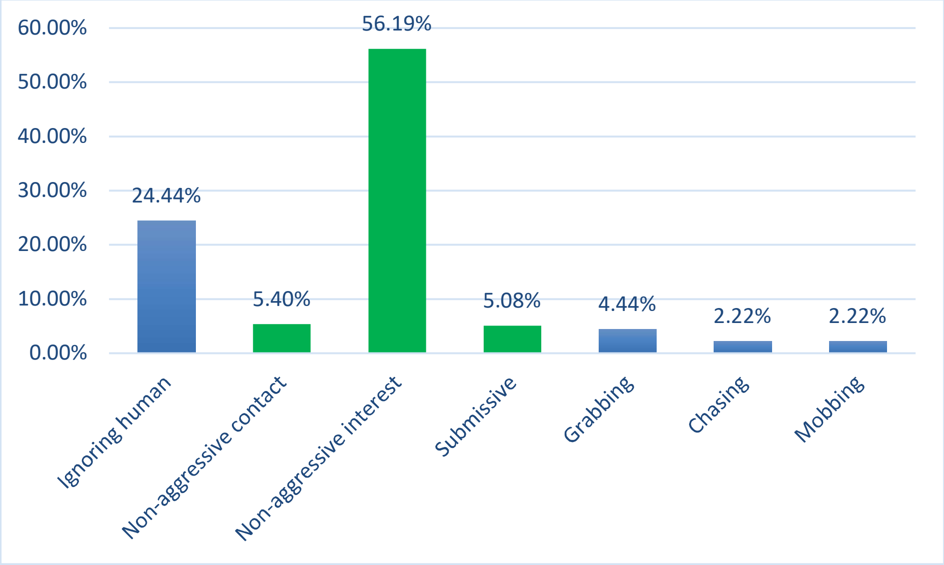

Figure 6: Affiliative/submissive vs aggressive macaque behaviour in human feeding contexts. Affiliative/submissive behaviours are (second from left) non-aggressive contact (N = 17), non-aggressive interest (N = 177) and submissive (N = 16), while aggressive behaviours included (from right) mobbing (N = 7), chasing (N = 7), and grabbing (N = 14). Macaques ignoring humans (N = 77) were also observed in human feeding but not analysed for interaction.

5.1.3 Rate of interactions during human provocation or retaliation contexts and the type of interactions

In human provocation or retaliation contexts, I predicted that affiliative or submissive macaque-to-human interactions would be observed at a higher rate than aggressive macaque-to-human interactions. Consistent with the prediction, the rate of aggressive macaque-to-human interactions (mean rank = 44.50) was significantly lower than the rate of affiliative or submissive macaque-to-human interactions (mean rank = 58.50) (U = 943.5, n1=51, n2=51, P = 0.001). The rate of aggressive macaque-to-human interactions (mean rank = 40.33) was also significantly lower than the rate of affiliative or submissive macaque-to-human interactions in human retaliation contexts (mean rank = 62.67) (U = 731.0, n1=51, n2=51, P = 0.001).

5.1.4 Rate of interactions during human-neutral contexts and the type of interactions

I predicted that in human-neutral contexts, affiliative or submissive macaque-to-human interactions would be observed at a higher rate than aggressive interactions. Consistent with the prediction, the rate of aggressive interactions (mean rank = 31.62) was significantly lower than the rate of affiliative or submissive interactions (mean rank = 71.38) (U = 286.5, n_1=51, n_2=51, P = 0.001).

5.2 Do interactions with humans differ between macaque demographic categories?

Across the demographic groups, most of macaque behaviour during encounters with humans consisted of macaques ignoring humans with adult males observed ignoring humans the most (Tables 4). Across contexts, sub-adult males interacted with humans the most, followed by females (Table 5).

Table 4: Mean (±SD) rate per focal hour of all macaque behaviour during encounters with humans by sex/age class. Affiliative/submissive type of behaviours in interactions included (second from left) non-aggressive contact, non-aggressive interest, and submissive behaviour, while aggressive type of behaviours included aggressive contact, grabbing, lunging, mobbing, and threatening.

Macaque sex/age class	Ignoring humans	Non-aggressive Contact	Non-aggressive Interest	Submissive	Aggressive Contact	Grabbing	Lunging	Mobbing	Threatening
Females	40.81 (12.20)	0.34 (0.64)	5.14 (4.02)	2.43 (1.82)	0.00 (0.00)	0.18 (0.46)	0.06 (0.20)	0.07 (0.21)	0.00 (0.00)
Adult males	42.57 (12.66)	0.00 (0.00)	3.33 (4.11)	0.75 (0.86)	0.00 (0.00)	0.57 (1.01)	0.08 (0.21)	0.13 (0.32)	0.15 (0.38)
Sub-adult males	40.22 (10.39)	0.57 (1.06)	9.02 (4.95)	2.99 (1.80)	0.00 (0.00)	0.80 (0.66)	0.00 (0.00)	0.19 (0.48)	0.20 (0.49)
Juveniles	33.02 (9.91)	0.03 (0.79)	2.86 (9.15)	1.63 (1.57)	0.00 (0.00)	0.09 (0.29)	0.18 (0.60)	0.07 (0.24)	0.00 (0.00)

Table 5: Mean (±SD) rate per focal hour of interactions by sex/age class across the contexts.

Macaque sex/age class	**All contexts**	**Human-neutral contexts**	**Human-initiated contexts**
Females	8.25 (5.62)	2.15 (1.78)	6.09 (4.82)
Adult males	5.03 (3.91)	2.76 (4.22)	2.27 (2.11)
Sub-adult males	14.29 (6.11)	3.11 (1.43)	11.18 (5.88)
Juveniles	4.61 (4.78)	1.93 (2.33)	2.67 (3.60)

All contexts=human-neutral contexts + Human-initiated contexts.
Human-initiated contexts=Human feeding + Human provocation + Human retaliation contexts (see Table 1).

5.2.1 Rate of interactions by sex/age class across human-initiated contexts

I predicted that adult and sub-adult males would interact with humans at a higher rate than females and juveniles do in human-initiated contexts (Table 5). There was a significant difference between demographic groups in interaction rate during human-initiated contexts (ANOVA: F (3, 47) = 7.760, P = 0.001). As predicted, sub-adult males interacted with humans significantly more than juveniles did in human-initiated contexts (Bonferroni multiple comparisons: P = 0.005, 95% C.I. = [3.22, 13.77]). Sub-adult males also interacted with humans significantly more than adult males in human-initiated contexts (P = 0.003, 95% C.I. = [2.26, 15.54]). However, contrary to the prediction there were no significant differences between females and males (sub-adult or adult) in human-initiated contexts. There was also no significant difference between adult males and juveniles in human-initiated contexts.

5.2.2 Rate of aggressive interactions by sex/age class across human-initiated contexts

I predicted that of the macaques that were observed in aggressive type of interactions with humans during human-initiated contexts, adult and sub-adult male macaques would be observed at a higher rate than female and juvenile macaques (Tables 6-7). There was a significant difference between demographic groups in aggressive type of interactions in human-initiated contexts (ANOVA: F (3, 47) = 4.943, P = 0.005). A Bonferroni multiple comparison indicated that, as predicted, sub-adult males interacted aggressively with humans significantly more than juveniles (P = 0.006, 95% C.I. = [0.25, 2.07]) and females (P = 0.014, 95% C.I. = [0.15, 1.97]) in human-initiated contexts. There were no significant differences between adult male macaques and female or juvenile macaques in human-initiated contexts. Thus, consistent with the predictions, sub-adult males were more likely, than other sex/age classes, to interact aggressively with humans in human-initiated contexts. Contrary to the prediction, adult males were not more likely than females or juveniles to interact aggressively with humans during human-initiated contexts.

Table 6: Mean (±SD) rate per focal hour of interaction type and context by sex/age class.

	Human-initiated contexts		**Human-neutral contexts**	
Macaque sex/age class	Aggressive interactions	Affiliative/ Submissive interactions	Aggressive interactions	Affiliative/ Submissive interactions
Females	0.32 (0.55)	5.78 (4.48)	0.00 (0.00)	2.15 (1.78)
Adult males	0.86 (1.09)	1.41 (1.70)	0.08 (0.21)	2.67 (4.27)
Sub-adult males	1.39 (1.11)	9.78 (5.39)	0.00 (0.00)	3.11 (1.43)
Juveniles	0.23 (0.63)	2.44 (3.06)	0.00 (0.00)	1.93 (2.33)

Table 7: Mean (±SD) rate per hour of interaction type and context by sex/age class across the human-initiated contexts, i.e., human feeding, human provocation, and human retaliation.

	Human feeding contexts		**Human provocation contexts**		**Human retaliation contexts**	
Macaque sex/age class	Aggressive interactions	Affiliative/ Submissive interactions	Aggressive interactions	Affiliative/ Submissive interactions	Aggressive interactions	Affiliative/ Submissive interactions
Females	0.32 (0.55)	4.45 (3.89)	0.00 (0.00)	0.34 (0.61)	0.00 (0.00)	0.96 (1.10)
Adult males	0.54 (1.00)	0.66 (1.03)	0.00 (0.00)	0.13 (0.32)	0.31 (0.76)	0.62 (0.76)
Sub-adult males	1.09 (1.12)	7.08 (5.01)	0.00 (0.00)	0.42 (0.79)	0.29 (0.51)	2.28 (1.78)
Juveniles	0.23 (0.63)	1.68 (2.24)	0.00 (0.00)	0.28 (0.51)	0.00 (0.00)	0.47 (1.09)

5.2.3 Rate of affiliative/submissive interactions by sex/age class across human-initiated contexts

I predicted that of the macaques that were observed in affiliative/submissive type of interactions with humans during human-initiated contexts, female and juvenile macaques would be observed at a higher rate than adult and sub-adult male macaques (Tables 6-7). There was a significant difference between demographic groups in affiliative/submissive interactions in human-initiated contexts (ANOVA: F (3, 47) = 7.907, P = 0.0001). Contrary to the prediction, sub-adult males were observed in affiliative/submissive type of interactions with humans significantly more than juveniles (P = 0.001, 95% C.I. = [2.57, 12.10]) and adult males (P = 0.002, 95% C.I. = [2.37, 14.36]) in human-initiated contexts. There were no significant differences between adult/sub-adult males and females in human-initiated contexts. Thus, contrary to the prediction, adult and sub-adult males were as likely as females and juveniles to be observed in affiliative/submissive type of interactions with humans during human-initiated contexts.

5.2.4 Rate of interactions by sex/age class across human-neutral contexts

I predicted that of the macaques that were observed in interactions with humans during human-neutral contexts, adult and sub-adult males would be observed interacting with humans at a higher rate than females and juveniles (Table 6). No significant differences were found in human-neutral contexts across the demographic groups (ANOVA: F (3, 47) = 0.538, P = 0.659), indicating that adult and sub-adult males were not more likely than females and juveniles to be observed interacting with humans in human-neutral contexts.

5.2.5 Rate of aggressive interactions by sex/age class across human-neutral contexts

I predicted that of the macaques that were observed in aggressive type of interactions with humans during human-neutral contexts, adult and sub-adult male macaques would be observed at a higher rate than female and juvenile macaques. In human-neutral contexts, only adult males were recorded in aggressive type interactions with humans (Table 6). However, contrary to the prediction, no significant differences were found across the sex/age class in human-neutral contexts (ANOVA: F (3, 47) = 2.765, P = 0.052).

5.2.6 Rate of affiliative interactions by sex/age class across human-neutral contexts

I predicted that of the macaques that were observed in affiliative or submissive type of interactions with humans during human-neutral contexts, female and juvenile macaques would be observed at a higher rate than adult and sub-adult male macaques. In human-neutral contexts, sub-adult males showed the highest rate of affiliative or submissive interactions with humans (Table 6). Contrary to the prediction, no significant differences were found across the sex/age class in human-neutral contexts (ANOVA: F (3, 47) = 0.505, P = 0.680).

Chapter 6

Discussion

In this study, I aimed to analyse macaque behaviour towards humans and various human-macaque interactions in Singapore, providing a perspective on the relationship of Singaporeans/tourists with macaques. I also aimed to address a gap to understand interactions based on macaque life history traits which to my knowledge has not yet been studied in Singapore.

6.1 In what context(s) do macaques interact with humans at a higher rate and what are the types of interactions?

Of all encounters, most were human-neutral, during which humans were either ignoring monkeys, e.g., jogging past, or slowing down to watch or photograph monkeys. The most common macaque behaviour that occurred in human-neutral contexts was monkeys ignoring humans. Instead, monkeys engaged in species-appropriate activities like resting, natural foraging, traveling, and socializing with conspecifics when ignoring humans. Human-macaque interaction events, particularly relating to human provisioning which are part of their activities, accounted for less than one-fifth of the overall encounters. This is consistent with earlier primate studies, such as O'Leary and Fa's (1993) that show that only 13% of observed activities in Barbary macaques in Gibraltar involved human-macaque interactions. Singapore study by Riley et al. (2016) observed that over 90% of macaque activities had no interactions between humans and the long-tailed macaques. This suggests that in the absence of human provisioning in human-neutral contexts, monkeys spend most of their time not interacting with humans while sharing space with humans.

The context under which most interactions occurred was human-initiated, where human behaviour, actions or activities trigger an interaction. This is consistent with my prediction and the closely related study by Sha et al. (2009) on the Singapore macaques. That humans are the main drivers of human-macaque interactions is also consistent with studies in other countries showing high rates of interactions within these contexts driven mainly by human provisioning (e.g., O'Leary and Fa, 1993; Wheatley and Harya, 1994; Sha et al., 2009; Ilham et al., 2017; and Balasubramaniam et al., 2020). I also observed a quarter of human-macaque interactions in human-neutral contexts. This is slightly more than but still aligns with the findings of Sha et al. in 2009. Taken together, this suggests that human-macaque interactions are not likely to occur except for human behaviour or actions triggering interactions, particularly human provisioning behaviour.

Across the contexts, the most common type of macaque-to-human interactions was affiliative, with a small number of aggressive interactions. This is consistent with previous studies in Singapore e.g., by Fuentes et al. (2008) and Sha et al., (2009). Human-neutral contexts showed a higher rate of affiliative or submissive macaque-to-human interactions than aggressive types, likely due to the absence of food involvement. Macaque aggression towards humans is frequently reinforced in human food provisioning contexts, as macaques are often rewarded for their aggression towards humans. In this study, I observed no aggressive contact and few non-aggressive contacts which is in stark contrast to other countries where over half of interactions in human feeding involved physical contact (e.g., O'Leary and Fa, 1993; Wheatley and Harya, 1994; Balasubramaniam et al., 2020).

I recorded only a small number of interactions in human provocation contexts, like Sha et al.'s 2009 study. In human provocation contexts, macaques exhibited more affiliative/submissive behaviour than aggressive behaviour in interactions, which was what I expected to see. This is because in these contexts, humans may appear to challenge monkeys by advancing close, pointing, taunting, producing loud verbal expressions, or laughing at monkeys, which could be perceived as a threat to monkeys and cause monkeys to retreat to safety. Provocation behaviour always challenges the recipient, whether it is intended or not. For example, because humans have a strong preference for interacting with mothers and infants, I often observed humans approach too close to monkeys in this sex/age group, pointing, waving, and talking excitedly. Monkeys may interpret these human gestures to be aggressive and threatening, and thus cause monkeys to retreat submissively taking their infants with them. Education is crucial for modifying human behaviour, promoting quieter approaches to wildlife, reducing excitement, and distinguishing between aggressive and submissive macaque behaviour, as humans often mistake fear grins for aggressive teeth-baring (Aldridge, 2015; Tan, 2017).

I found that most human-macaque interactions occurred in human feeding contexts involving human provisioning, as per most studies (e.g., O'Leary and Fa, 1993; Wheatley and Harya 1994; Sabbatini et al.,2005; Sha et al., 2009; Hsu et al., 2009; Ilham et al., 2018; Morrow et al., 2019; Balasubramaniam et al., 2020). Sha et al. (2009) reports over two-thirds of interactions involved both direct and indirect human provisioning in Singapore. In Sha's study, indirect provisioning involves macaques responding to feeding cues, such as humans holding plastic bags which macaques associate with human food. As the law against wildlife feeding in Singapore has become stricter since Sha's study, human feeding in this study was much more likely to have occurred in indirect than direct provisioning. Feeders caught directly feeding wildlife, not just within the park but now also outside the park, can face fines of up to S$50,000 or imprisonment (Iau, 2019).

At the time of my observations, indirect provisioning occurred when humans were eating or have finished eating their food e.g., at an outdoor hawker centre or a picnic in the park. The Mushroom Café, an Alfresco-style outdoor food centre, was the primary location where I observed most indirect provisioning events. Monkeys frequently waited near tables, monitoring human diners for opportunities to grab food after humans have left. Humans generally ignored monkeys, some appreciated them from their tables, while others began retaliating to prevent them from taking their food. Indirect feeding also occurred when macaques foraged in human food trash at the café, and during other human activities such as picnics in the park and when humans were observed carrying plastic bags which macaques associate with human food. This mostly occurred on footpaths around the park and at the main local bus stop. The Singapore government has initiated charging single-use plastic bags. People should be encouraged to adopt the use of alternative carriers or bags that monkeys do not associate with food. I observed only two instances of direct provisioning, one group of people secretly throwing monkeys bread when cycling past and another group feeding monkeys grapes and bananas from plastic bags. The second group of people looked like tourists and might not have been aware of the strict feeding laws. Residents are less likely to feed macaques than visitors since they are more likely than visitors to be aware of the feeding ban (Sha et al., 2009).

In human feeding contexts, I found macaques exhibited more affiliative/submissive behaviour than aggressive behaviour, which was not as expected. Previous studies suggest that food provisioning has led to increased aggression among primates towards people, indicating that monkeys may exhibit more aggression than affiliation in this context (e.g., O'Leary and Fa, 1993; Wheatley and Harya, 1994; Hsu et al., 2009). Instead of this, macaques most often displayed non-aggressive interest towards humans in human feeding contexts. Although Sha et al. (2009) also reports that the most common macaque-to-human interactions were affiliative/submissive, the authors do not specify the contexts in which they occur. Aggressive behaviours in Sha's study, including grabbing and taking belongings, accounted for over a third of macaque behaviour in interactions, contrasting with only one of a hundred in this study. It may be important to mention that I observed only a single monkey snatching food while humans were eating at a table. The same individual also repeated the behaviour when a group of humans were having a picnic in the park. Neither event involved direct skin contact. These events demonstrate that aggression may be driven mainly by one or two individuals, making it ungeneralizable across the population (Sabbatini et al., 2005). The media often sensationalize macaque attacks (Tan, 2016; Ang, 2021), but it is crucial that news reports clarify that these incidents are anomalies rather than the norm.

Linking to human feeding are a small number of interactions I observed in human retaliation contexts. Human retaliation involves human response to macaques attempting to invade their space or steal their belongings during human feeding events, such as chasing, yelling, or waving a stick. In human retaliation contexts, I observed mostly affiliative/submissive macaque-to-human interactions, which was as expected. For instance, I expected monkeys would choose to avoid confrontations with humans and run away due to their larger size, and the various human behaviours perceived to be threatening to the monkeys. In the Mushroom café where I observed most retaliation events, the food vendors displayed most of this retaliatory behaviour, likely to safeguard their customers and their business. Singapore's public education campaigns teach monkey avoidance, including monkey guarding, which involves blocking and deterring monkey approaches with assertiveness (NParks, 2023). In the study, monkeys generally retreated from the humans when this occurred, possibly indicating the success of the program. Most of the time, monkeys wait with non-aggressive interest. I recorded only once a macaque's aggressive response to a customer, which demonstrates that human assertiveness may be perceived as aggression by monkey and also lead to a reciprocal aggressive response (Beisner et al., 2015). However, this is not universal but typical of only one or two individuals (Sabbatini et al., 2005). Education can help people understand natural monkey behaviour, including distinguishing between aggressive and submissive displays, as people may often mistake snarling for fear grin and vice versa (Aldridge, 2015; Tan, 2017).

Sha et al., (2009) suggests that factors like location, history, physical space overlap, hunger, thirst, and seasonal changes can significantly influence macaque-human interaction and behaviour, and macaque motivation to access human food may also be influenced by past experiences with human feeding or harassment. For instance, the implementation of higher fines for feeding macaques and stricter enforcement is likely to have considerably reduced direct human provisioning, at least in full public view at the time of my observations. Continuous public education may have increased human caution in not carrying food cues that macaques respond to, and learning to deter monkeys using sticks or noise-making techniques. Human assertiveness, perceived as aggression by monkeys, may have led monkeys to flee in submission. On the other hand, monkeys displaying cautiousness with non-aggressive interest during human feeding opportunities may serve to demonstrate the opportunistic nature of their foraging strategies.

6.2 Do interactions with humans differ between macaque demographic categories?

6.2.1 Human-initiated contexts

I expected sub-adult males to interact with humans more than females and juveniles. This was the case in my study. This supports the life history theory's prediction that sub-adult males are more prone to risk-taking, aligning with past research on various primate species and wildlife populations in anthropogenic environments (Sabbatini et al., 2005; Chiyo et al., 2012; Fehlmann et al., 2017; Lischka et al. 2018; Morrow et al., 2019; Balasubramaniam et al., 2020). Sub-adult males possess reproductive potential but must compete with higher ranking males for mates, requiring significant energetic costs due to increased agonistic and sexual activities in their strict dominance hierarchy society (Gesquire et al., 2011; Morrow et al., 2019). In social network and centrality studies, sub-adult males, who are less centrally connected and more spatially peripheral than the other demographic groups, tend to engage in interaction with humans more than females or juveniles (Morrow et al., 2019; Balasubramaniam et al., 2020). Additional to being at the point of dispersal to avoid male-male competition as well as inbreeding (Lute et al., 2014), peripheralized sub-adult male individuals may also exhibit increased risk-taking behaviour due to their exploratory and bold personality (Morrow et al., 2019; Balasubramaniam et al., 2020).

Linking to this, sub-adult male macaques also engaged the most in aggressive interactions with humans in human-initiated contexts, which also aligns with previous research (e.g., O'Leary and Fa, 1993; Sabbatini et al., 2005; Hsu et al., 2009; Morrow et al., 2019; Balasubramaniam et al., 2020). Human behaviour influenced by life history traits may also help explain this behaviour. Male primates tend to be less favoured by humans for interactions than females with infants, and juveniles. Because of this, males may exhibit increased inter-species aggression, particularly in human feeding contexts to obtain anthropogenic food (O'Leary and Fa, 1994; Fuentes and Gamerl, 2005). However, unexpectedly, sub-adult males also exhibited the most affiliative/submissive behaviour in human-initiated contexts. This may partly be linked to human retaliation contexts which often follow human feeding contexts in triggering macaque behaviour. As sub-adult male macaques are more likely to risk obtaining human food, they would be more likely to be observed more frequently retreating from humans in human retaliation contexts. My findings seem to suggest this may be the case, as the rate of affiliative/submissive behaviour among sub-adult males is higher than the other demographic groups during human retaliation. However, sub-adult males also had the highest rate of affiliative/submissive behaviour in human provocation contexts. Since sub-adults interacted with humans the most across all the contexts, this may influence the rate of interaction leading to higher overall rates across the different human-initiated contexts.

Among adult male macaques, I observed adult males ignore humans more than the other demographic groups in all encounters, even when humans stopped nearby to watch the monkeys. An encounter may or may not lead to an interaction. When a monkey ignores the human, an interaction does not take place. This macaque behaviour seems to be overlooked in studies, although it may be part of the macaque activity budget (e.g., O'Leary and Fa, 1993 and Riley et al., 2016; Ilham et al., 2017). Indeed, the observed behaviour mostly coincided with monkeys engaging in grooming, locomotion, or foraging non-anthropogenic food sources. Future research could integrate macaque behaviour towards humans with activity budget to establish a relationship to compare studies.

Where encounters led to an interaction, contrary to my expectation, adult males did not engage in human-macaque interactions more than females or juveniles in human-initiated interactions. Ignoring humans more than the other sex/age groups likely contributed to the lower rates of interactions among adult males, as they did not engage in any interactions while exhibiting the behaviour. Another plausible explanation for the lower rate of interaction may be because macaque sex/age class differences may also influence human behaviour. Humans generally prefer to interact with infants and juveniles and may have avoided adult males due to their larger body size (O'Leary and Fa, 1993; Sabbatini et al., 2005). The low human-macaque interaction rate among adult males may not suggest adult males are risk averse, however, like the females or juveniles. Rather, not retreating from humans may be risky, indicating their level of confidence and boldness supporting life history theory. For instance, in many of these encounters, I observed adult males resting, sometimes in the middle of a footpath, forcing humans to walk around them. On other occasions, adult males were often the recipient of allogrooming. Monkeys' lack of response to human presence may suggest they view humans as just a factor of their environment, like how most wildlife may perceive humans (Goumas, 2020).

Adult males also displayed less aggression and more affiliation towards humans than expected. Adult males are high-ranking individuals with higher reproductive success and quality of offspring, but acquiring and maintaining dominance requires significant energetic costs due to increased sexual and agonistic activities (Gesquire et al., 2011; Morrow et al., 2019), so one would expect adult males to exhibit behaviours to reflect this. There may be a few possible explanations. Adult males may be experiencing increased intra-group competition, e.g., from bolder, more aggressive sub-adult males seeking to assert their dominance. This may have contributed to the higher rates of macaque-to-human interaction by sub-adult males, including aggressive interactions. However, this may be unlikely as studies indicate that peripheralization of males is less likely to result from intra-group aggression between adult and sub-adult males due to low aggression rates reported (Lute et al., 2014). Males may be experiencing increasing pressures due to being in a large macaque group, which may be more plausible. Previous research has revealed that populations with higher anthropogenic resource access often grow rapidly, surpassing the habitat's capacity to sustain the population (Sugiyama, 2015). This results in increased intra-species aggression and agonistic interactions, leading to high infant mortality (Wheatley et al., 1994). Indeed, field assistant Simpson's video recordings reveal fights taking place between an adult male from the larger macaque group and members of the smaller group. The adult male regularly sought to join the smaller group that had only a single adult male, sustaining injuries indicating agonistic interactions with the other macaques. Another male from the larger group had previously attempted to cross over, as reported by Simpson, but had remained mostly at the periphery of both macaque groups during the study. Males must assess their circumstances, consider factors such as affiliations, group stability, and adjacent group dynamics and weigh the cost benefit of engaging in intra-specific agonistic interactions (Lute et al., 2014). It may be possible that such competition pressures have distracted adult males from engaging more with humans in interactions.

Amongst female macaques, I found that females showed more interactions with humans than adult males in human-initiated contexts, particularly in human feeding category. This was contrary to life history theory where females are more risk averse due to high reproduction costs and greater potential for loss (Clark, 1987; Roff, 2002; Rueffler et al., 2004; Wolf, 2009). Further, given Singapore’s strict laws against direct human provisioning at the time of the study, direct provisioning is unlikely to be the reason for the high rate of human-macaque interactions amongst females in human feeding. Human feeding was more likely to have occurred during indirect provisioning. During data collection, I often witnessed a few female individuals, sometimes with infants, actively engaging in bold exploratory behaviours at the Mushroom café and the bus stop. On one occasion, an older female macaque retrieved a milk carton dropped by a human who was fleeing from her. This is an example of how macaque aggression is frequently unintentionally reinforced when they are rewarded for their aggression towards humans (O'Leary and Fa, 1993). Although contrary to expectations that females are risk averse, studies have also suggested that female macaques may display increased aggression and reliance on anthropogenic food during offspring rearing, to protect and meet the energetic demands of their offspring (Fa, 1992; Beisner et al., 2015). This may be the case here. To discourage monkey approach, people should be more assertive with females and juveniles, avoid close interactions, especially during offspring rearing, and appreciate monkeys more from a distance.

Life history traits influencing human behaviour may also help explain the high rate of interaction amongst female in human feeding contexts. Historically, humans tend to favour adult female monkeys with infants and juveniles as provisioning targets (Sabbatini et al., 2005), and it was possible that females have experienced this and expected it (Fuentes, 2008; Sha et al., 2009). Although the prohibition of direct provisioning of monkeys has led to a decrease in direct provisioning (Iau, 2019), adult female monkeys, driven by the requirements of offspring rearing, may still approach humans with the expectation of direct provisioning learned when provisioning was more prevalent (e.g., Sha et al., 2009). Female macaques also showed a high rate of affiliative/submissive behaviour in human retaliation contexts, which is consistent with life history traits. However, as already shown, females were as likely as sub-adult males to engage in interactions in human feeding contexts. This being the case, they were also as likely as sub-adult males to be observed retreating from humans when humans retaliated. In human provocation contexts, I have observed humans approach female monkeys with infants too closely, pointing and waving and talking loudly and excitedly. These expressive human gestures which may be interpreted by macaques to be aggressive often led female monkeys to retreat submissively taking their infants with them. Education is key for modifying human behaviour, including keeping a distance, approaching wildlife slowly, reducing excitement, and avoiding behaviour that might be perceived as threatening to monkeys (Tan, 2017).

Finally, my findings on juvenile macaques showed that juveniles interacted with humans the least across the demographic groups, which was expected based on life history traits. This is because juveniles may face higher mortality risks due to their smaller body size, making them more risk averse (Dunbar, 1987; Promislow and Harvey, 1990; 1990; Janson et al., 2002). Further, although humans like to single out cuter younger monkeys, older, sedentary monkeys are often easier to interact with due to their tolerance for close contact, while younger monkeys are more active and seldom remain still long enough for interactions (O'Leary and Fa, 1993; Sabbatini et al., 2005). This may also have contributed to the lower rate of interactions among juveniles. However, I also recorded juveniles ignoring humans the least of all the demographic groups. The contradictory data suggests that there were fewer macaque juvenile-human interactions overall. Future studies could ensure balanced presentation across the demographic categories.

6.2.2 Human-neutral contexts

In human-neutral contexts, based on life history predictions, I expected to see adult and sub-adult males interact with humans more than females and juveniles. This is because adult and sub-adult males are more risk-prone and likely to engage with humans for anthropogenic food gains than females and juveniles, who are more risk averse. However, this was only true of sub-adult male macaques. Adult males interacted with humans more than juveniles, as expected, but less than females. As already seen, adult males ignored humans more than the other groups which likely led to a lower overall rate of interactions than sub-adult males and females.

Also contrary to life history expectations, male macaques were as likely as females and juveniles to exhibit affiliative behaviour towards humans in interactions. Macaques have shown interest in humans in human-initiated contexts when humans provide indirect alternative food sources to meet their energetic needs, e.g., at the Mushroom Café. As human-neutral contexts lack human food involvement, macaques were less likely to interact with humans because of this. Further, the absence of human provisioning towards females and juveniles also reduced the need for male macaques to aggress against humans or conspecifics in competition over anthropogenic food sources. As humans historically prefer to provision females with infants and juveniles, in the absence of food provisioning, there is no motivation to aggress against humans by the males.

Although adult males did not engage in aggressive interactions with humans more than females on juveniles, which was unexpected, the lower overall rate of interaction with humans may have contributed to this anomaly. Further, I recorded only one instance of aggression by a single adult male. The behaviour was unprovoked since humans did not cause the interaction other than being in proximity. Environmental factors may have triggered the interaction. Nevertheless, as shown in human-initiated contexts, the lack of engagement or aggression with humans may be explained by the distractions experienced by adult males at the time of my study, i.e., intra/inter-group competition. It is possible the same can be applied to this one-time unprovoked aggression directed at humans in human-neutral contexts. Adult males face increased competition pressure from bolder, more aggressive sub-adult males seeking to assert their dominance. Males also face inter-group aggression from conspecifics asserting themselves to maintain their own dominance. Education can help better understand macaque behaviour and avoid confrontations or interactions with them, including excessive closeness during intraspecific aggression (Tan, 2017).

Some macaques initiated affiliative interactions in human-neutral contexts. During observations, I watched a sub-adult male macaque grooming a human's leg in an interaction initiated by the macaque. The human tolerated the macaque's grooming, remaining still and appearing familiar with its presence. At another event, I observed a group of macaques resting, socializing, and foraging next to a couple sitting on a park bench. A juvenile hopped onto the bench arm and made a gentle, play like contact with one of the humans. I also did not observe either human initiating the interaction. These events may serve as examples of monkeys initiating interactions through associative learning (O'Leary and Fa, 1993). Associative learning is a cognitive process where monkeys associate specific objects, people, or actions with specific rewards and outcomes, such as non-threatening humans, and initiate interactions through proximity, touch, or jumping on them (Hsu et al., 2009). The macaques were familiar with the humans, exhibiting familiar behaviour, suggesting they had seen them and interacted with them on multiple occasions. Positive human-wildlife interaction has many benefits, including enhancing conservation success and improving human wellbeing. Nevertheless, close, direct contact interaction with wildlife should be discouraged to minimize risks of injuries, and zoonotic / anthroponotic diseases.

6.3 General Discussion

My findings indicate that Singapore is mostly a peaceful environment for both humans and macaques and that the co-occurrence of humans and macaques may not always be a problem requiring interventions. Of the 2,703 human-macaque encounters recorded, I observed monkeys ignoring humans in 83.17% of the encounters. Only 16.83% of encounters involved macaque-to-human interaction. This suggests that monkeys view humans as a mere inconsequential part of their natural environment. Macaques also largely ignored humans when human food was absent. As most interactions occur in contexts initiated by humans involving human food, reducing, or eliminating human food availability is key to reducing problematic interactions. Upon visiting the study site in 2023, I discovered that the lease on the Mushroom Café has not been renewed (see Figure 7), possibly due to their attraction to monkeys (bystander comment). The once bustling eatery visited by both humans and macaques now stood empty. Nevertheless, with the removal of a significant anthropogenic food source from the macaques' feeding ground, most of the macaques I observed then were now in the forest and surrounding trails, although I have not collected the data for it. It may be timely for further study to examine how interactions with humans have changed now that a source of anthropogenic food has been removed from the environment.

Figure 7: The Mushroom café, April 2023 (Author, 2023).

Macaques exhibited more affiliative/submissive behaviour than aggressive behaviour in interactions involving human food, even for male macaques. This suggests that macaque motivation to access human food may be influenced by past experiences with human feeding or harassment (Sha et al., 2009). Monkeys may exhibit cautious behaviour due to increased human assertiveness, which they perceive as aggression, and err on the side of caution to avoid human retaliation. Adult female macaques were also involved in many interactions more than expected, even more than adult males and juveniles, but this anomaly has been observed in some primate species (e.g., Fa, 1992; Beisner et al., 2015). Females may exhibit increased reliance on anthropogenic food during offspring rearing to meet their energetic demands, leading to increased food related interactions (Balasubramaniam et al., 2020).

Although I observed many humans ignore the monkeys, it was heartening to observe that it was largely not due to a fear of monkeys. That the humans were not disturbed by the monkeys, but were used to their presence, demonstrates that both species cohabit in shared spaces without issues. Visitors to the nature park are typically residents or regular park users, such as runners, who are likely used to their presence. Non-resident visitors tend to visit the site to appreciate nature and observe wildlife. Indeed, many encounters involving humans appreciating monkeys confirmed this. Only a small minority were observed in interactions involving provisioning, suggesting the Singapore strategy to reduce human feeding have been mostly successful.

6.4 Limitations and recommendations

The study has a few limitations, including not personally recording macaque videos and relying on third-party input. My findings might be more robust if I had personally visited and collected firsthand footage and information. For example, the accuracy of gauging human-macaque proximity on video is reduced due to the lack of depth of field and optimal angle position for accurate measurements. Further, Simpson's commentary providing data on human presence in videos as well as other data was often hindered by ambient noises which impeded more accurate interpretation. The study's sample is small, necessitating the combination of two macaque groups. A larger sample can yield more meaningful statistics, enabling more generalizable potential across the species' population. Equally, studying multiple macaque groups can facilitate better comparisons between groups to analyse variations in interaction. Although research indicates larger groups tend to have more access to anthropogenic food (e.g., Wong and Ni, 2000), many instances of resource access involved individuals from the smaller group, which also appeared more cohesive in defending themselves against outsiders. The sample sizes might not be equal across the focal individuals, with some individuals being underrepresented and others overrepresented. I overcame this limitation by computing the rate of behaviour instead of the overall frequency when analysing demographic differences, but it may still have hindered a more accurate analysis.

Future research incorporating social network analysis can help understand how social characteristics within the local populations influence group-wide patterns in resource access and risk-taking tendencies, such as dominance rank, connectedness, and spatial position (Balasubramaniam et al., 2020). Social network studies may reveal if closely affiliated macaque individuals display similar patterns of interaction with humans or the likelihood of interactions with other macaque partners than alone (Morrow et al., 2019). Alongside this, integrating personality type studies can offer valuable insights at individual, group, and collective levels (Carter et al., 2013). For instance, life history theory suggests sub-adult males are risk-prone, while females are risk-averse (Balasubramaniam et al., 2020). Social network studies reveal less connected, spatially peripheral sub-adult males engage in more human interaction, while more centrally connected females tend not to (Morrow et al., 2019). Life history theory also suggests that males tend to exhibit bolder, more aggressive behaviour than females (Hsu et al, 2009). However, as revealed in my findings, this is not always the case. Thus, understanding personality types may help shed some light on how individuals overcome life history traits and social characteristics to interact with humans. My findings also suggested that sub-adult males exhibit the highest rate of aggressive interactions with humans compared to adult males and other sex/age classes. Future research should investigate if this is due to the human-macaque dynamic or if individuals in this sex/age class also interact with conspecifics more aggressively than those in other sex/age classes.

My study revealed that residents and visitors alike show high tolerance and appreciation for monkeys, suggesting that public perception of macaques may be positive. However, Sha et al. (2009) conducted a study using quantitative tools such as questionnaires and media headlines to gauge public perceptions and found that they were more negative than positive of macaques. Complaints against macaques were also primarily made by residents who view monkeys more negatively than visitors. It may be prudent to revisit Sha et al.'s (2009) study to ascertain what the current prevailing societal perceptions are based on media connotations. Further, to achieve long-term peaceful coexistence, it is essential to address social mismatches among different human groups (Hill, 2015), as disagreements often arise from differing viewpoints regarding wildlife protection (Setchell et al., 2017). However, quantitative tools, as used by Sha et al. (2009), may lack nuanced understanding of influences, such as social and cultural influences, on human perception of wildlife (Setchell et al., 2017). Conversely, qualitative ethnographic techniques like participant observation and semi-structured interviews may provide more comprehensive understanding that help foster shared views, empathy, and cooperation (Orlove and Brush, 1996; Setchell et al., 2017). Research on how people perceive monkeys in situations where humans and monkeys are at odds is still relatively in its infancy (Hill, 2015). Thus, future research through bio-social approaches could be adopted to enhance our understanding of public perception of macaques (Setchell et al., 2017). The success of management initiatives in problemed interfaces hinges on understanding people's perceptions of monkeys as “nuisance” which allows for the development of management practices that specifically address the concerns of residents (Hill, 2015).

6.4.1 Management Implications

Negativity bias in Singapore's newspaper reports reveal a persistent lack of tolerance towards macaques, with media headlines presenting public perception of macaques more negatively than positively (Sha et al., 2009). It is time to include more positive stories involving positive psychology to enhance wildlife experiences and protection, which can boost conservation success by identifying beneficial mechanisms (Buijs and Jacobs, 2021). The media frequently sensationalizes macaque and other wildlife attacks (e.g., Tan, 2016; Ang, 2021), but it is crucial to clarify that these incidents are anomalies rather than the norm, as indicated by my findings. Education is crucial for modifying human behaviour towards monkeys, promoting quieter approaches, containing excitement, and distinguishing between aggressive and submissive macaque behaviour (Tan, 2017). Since the Singapore government has initiated charging single-use plastic bags, people should be encouraged to adopt the use of alternative carriers or bags that monkeys do not associate with food. Training individuals identified with high connectedness and dominance rank, as well as spatially peripheral bold individuals, e.g., through monkey guarding, may enhance management practices. Nevertheless, with the removal of a significant anthropogenic food source from the macaques' feeding ground in MacRitchie Reservoir Park, i.e., the Mushroom café, interactions with humans could be more positive as my study suggests. However, further research to collect new human and macaque behaviour data may be useful to determine this.

Chapter 7

Conclusion

Anthropogenically altered environments are leading to more human-wildlife contact. Understanding sympatric relationships between humans and primates is key to managing the human-primate interface. My study adds to a body of evidence that promotes positive psychology, showing that humans and macaques can coexist peacefully in shared environments and that their co-occurrences are not always a challenge needing intervention. The literature on primate behaviour in human-macaque interface often discusses conflict, neglecting positive relations, which poses challenges to wildlife management. Research focusing on conflict may overemphasize negative aspects of human-macaque interactions hindering conservation success. Conversely, positive psychology can promote benefits and identify mechanisms that make wildlife experiences and protection more meaningful, ultimately optimizing conservation success. Coexistence is a sustainable relationship between humans and wildlife, governed by laws to protect wildlife population longevity and manage tolerable risks. Recognizing humans as a solution for positive human-wildlife coexistence promotes tolerance and understanding that wildlife and humans can thrive together in shared landscapes. To understand human-primate interactions better, more accurate, all-encompassing and comprehensive documentation and systematic study of the human-primate interface is required by gathering data for all types of behaviour and interaction, including positive, neutral, as well as problematic ones.

The Singapore media frequently sensationalizes macaque and other wildlife attacks, emphasizing a negativity bias, but it is crucial to recognise that these incidents are not the norm. As revealed in the study, residents and visitors show high tolerance and appreciation for monkeys, suggesting a positive public perception of macaques, with positive or neutral interactions far outweighing negative ones.

Moreover, problematic interactions between humans and macaques are mostly caused by a few individuals and cannot be generalized across populations. Education is thus key for modifying human behaviour towards monkeys, including stricter enforcement to discourage feeding monkeys and encouraging alternative carriers that monkeys may not associate with food. Further, understanding personality types can provide insight into how some macaque individuals overcome life history traits and social characteristics to interact with humans. Selectively targeting influential macaque individuals for behaviour modification training can teach them to avoid human interaction, potentially spreading this behaviour to the entire macaque population.

Appendix A

Table 1: Raw encounter and interaction frequency data for individual macaques (columns A to I) and interaction rates per focal hour for macaque behaviour (columns J to M).

	A	B	C	D	E	F	G	H	I	J	K	L	M
Id	Sex	Age	Total sample minutes	Total encounters recorded	Encounters with no interaction (ignoring humans)	Encounters with interactions	Interaction frequency in neutral contexts	Interaction frequency in human initiated contexts	Interaction frequency in human feeding contexts	Rate of interaction in human neutral contexts	Rate of interactions in human initiated contexts	Rate of affiliative /submissive behaviour in human feeding contexts	Rate of aggressive behaviour in human feeding contexts
ANG	F	Adult	60	42	24	18	4	14	13	4.00	14.00	13.00	0.00
BON	M	Adult	114	101	93	8	2	6	4	2.00	6.00	4.00	0.00
BRU	M	Juvenile	48	25	18	7	6	1	1	6.00	1.00	1.25	0.00
CHL	F	Juvenile	62	41	40	1	1	0	0	1.00	0.00	0.00	0.00
CLA	F	Juvenile	42	33	31	2	2	0	0	2.00	0.00	0.00	0.00
DOL	F	Adult	54	69	54	15	1	14	12	1.00	14.00	11.00	1.00
DUC	F	Adult	48	19	19	0	0	0	0	0.00	0.00	0.00	0.00

DUK	F	Subadult	60	50	34	16	7	9	9	7.00	9.00	9.00	0.00
ELS	F	Adult	54	40	37	3	2	1	1	2.00	1.00	1.00	0.00
ELT	M	Subadult	50	38	26	12	1	11	9	1.00	11.20	8.00	1.00
FER	F	Juvenile	70	67	50	17	1	16	11	1.00	16.00	8.00	3.00
FIG	F	Adult	106	103	90	13	5	8	7	5.00	8.00	6.13	0.00
FLU	M	Juvenile	54	25	20	5	4	1	0	4.00	1.00	0.00	0.00
FRA	M	Adult	70	73	60	13	13	0	0	13.00	0.00	0.00	0.00
FRO	F	Juvenile	102	58	58	0	0	0	0	0.00	0.00	0.00	0.00
HAY	F	Juvenile	50	20	18	2	1	1	0	1.00	1.00	0.00	0.00
JUA	F	Adult	122	145	122	23	5	18	11	5.00	18.00	9.49	1.00
JUL	M	Adult	76	44	41	3	0	3	1	0.00	3.00	0.00	1.00
KEN	M	Juvenile	50	33	29	4	2	2	2	2.00	2.00	2.00	0.00
KNO	M	Adult	64	45	37	8	2	6	2	2.00	5.94	2.00	0.00
LIO	M	Subadult	58	43	36	7	2	5	3	2.00	5.00	3.00	0.00
MIL	M	Subadult	102	66	45	21	4	17	10	4.00	17.00	5.59	4.00
JES	F	Subadult	66	39	31	8	3	5	4	3.00	5.00	4.00	0.00
LOV	M	Juvenile	42	22	21	1	0	1	0	0.00	1.00	0.00	0.00
JOL	F	Adult	68	43	31	12	2	10	6	2.00	10.00	5.00	1.00
BEC	F	Adult	64	30	23	7	2	5	3	2.00	5.00	3.00	0.00
BAT	F	Juvenile	66	42	34	8	3	5	4	3.00	5.00	2.91	1.00
BEE	F	Juvenile	54	23	20	3	1	2	1	1.00	2.00	1.00	0.00
JAM	M	Subadult	76	91	68	23	7	16	14	7.00	16.00	11.79	2.00
ERI	M	Juvenile	50	15	15	0	0	0	0	0.00	0.00	0.00	0.00
BOR	M	Adult	60	28	28	0	0	0	0	0.00	0.00	0.00	0.00
AND	M	Juvenile	46	19	19	0	0	0	0	0.00	0.00	0.00	0.00
ASA	F	Juvenile	62	75	58	17	8	9	8	8.00	9.00	6.94	1.00
COC	F	Juvenile	90	57	54	3	1	2	2	1.00	2.00	2.00	0.00
CHI	F	Adult	76	73	61	12	3	9	9	3.00	9.00	6.79	2.00
KOR	F	Juvenile	106	91	83	8	2	6	4	2.00	6.00	4.00	0.00
LUI	M	Subadult	44	40	35	5	3	2	1	3.00	2.00	1.00	0.00
LIZ	F	Subadult	60	38	37	1	0	1	1	0.00	1.00	1.00	0.00

MAR	M	Subadult	68	78	51	27	4	23	18	4.00	23.00	18.00	0.00
MEG	F	Adult	56	48	45	3	0	3	1	0.00	3.00	1.00	0.00
MAB	F	Adult	90	75	67	8	2	6	6	2.00	6.00	6.00	0.00
ROB	M	Juvenile	68	36	32	4	1	3	3	1.00	3.00	3.00	0.00
MOR	F	Subadult	52	47	44	3	2	1	1	2.00	1.00	1.00	0.00
TAY	F	Subadult	104	83	62	21	8	13	10	8.00	13.00	9.00	1.00
TIP	M	Subadult	118	112	78	34	6	28	18	6.00	28.00	13.00	5.00
LIV	F	Subadult	54	45	39	6	3	3	1	3.00	3.00	1.00	0.00
TIM	M	Juvenile	56	34	34	0	0	0	0	0.00	0.00	0.00	0.00
TER	F	Adult	114	138	107	31	2	29	21	2.00	29.00	17.05	3.00
VIL	M	Juvenile	52	34	26	8	2	6	4	2.00	6.00	4.00	0.00
REG	F	Adult	58	41	39	2	0	2	1	0.00	2.00	1.00	0.00
PAU	M	Adult	24	26	24	2	1	1	1	1.00	1.00	0.00	1.00
			1729	2703	2248	418	131	324	238				

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