Chapter 4
Rethinking Tolerance to Tourism: Behavioral Responses by Wild Crested Macaques (*Macaca nigra*) to Tourists

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Abstract There is an assumption that apparent tolerance of tourists at long-running primate tourism sites indicates habituation and that as a result primates no longer experience negative consequences of prolonged exposure to visitors. We examined effects of tourist presence on stress-related behavior in three groups of critically endangered, wild crested macaques (*Macaca nigra*) exposed to different intensities of tourism in Tangkoko Nature Reserve, Sulawesi, Indonesia. Group R2 has been exposed to research + intensive tourism for over 3 decades, R1 to research + less intensive tourism (1 decade), and PB1 to research only. Almost 740 h of data were collected from 33 adults via focal animal, all occurrence, and 1/0 sampling. All data were analyzed with general linear mixed models. Behavior appeared to be inhibited when tourists were in the forest, but not within groups; all groups vocalized less, exhibited fewer sexual behaviors and displayed fewer self-directed behaviors in months with greater numbers of tourists. When tourists were present vs. absent within groups, females displayed less affiliation, and males and females displayed more aggression, consistent with responses to uncertainty in the presence of tourists. Our results indicate that crested macaque groups exposed to tourism even for decades may not fully habituate to tourists. We tentatively suggest that their behav-

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ioral responses to tourists resemble typical responses of primates to perceived predators posing varying degrees of risk.

Keywords Stress-related behavior · Wildlife tourism · Primates · M. nigra · Tolerance · Aggression · Self-directed behaviors · Predator avoidance

4.1 Introduction

Many wildlife tourism operations that feature nonhuman primates aim to conserve ecosystems, financially benefit local populations, and educate both local people and visitors. Some ecotourism sites have been in operation for many years, often decades. Their target primate species appear to be habituated to tourists, influencing managers, and, at some sites, researchers as well, to assume that the local primate species no longer experience any negative consequences of prolonged exposure to visitors. However, this assumption of habituation is not necessarily accurate, and serious anthropogenic stressors sometimes accompany ecotourism.

4.1.1 Stress and Primate Tourism

Stress is an adaptive response to a perceived threat to survival, i.e., a stressor (Moberg 2000). However, prolonged or frequent exposure to stressors can be maladaptive due to the harmful physiological effects of prolonged or frequent exposure to certain hormones (e.g., glucocorticoids) that are released in response to stressors (Munck et al. 1984; Sapolsky 1992). Thus, uncovering specific prolonged or frequent sources of stress in ecotourist locations is vital. Of important note, glucocorticoids are metabolic hormones which do not function primarily as stress hormones (Beehner and Bergman 2017). Regardless, they are often elevated during exposure to stressors and are widely used as a proxy for the strength of an organism's response to stressors. Measuring potential physiological stress responses under varying conditions is one way to uncover sources of anthropogenic stress in ecotourist sites.

While physiological stress can be measured through various bodily substrates, some sources can be challenging to collect in wild and semi-wild habitats (Sheriff et al. 2011). Thankfully, researchers have connected increases in physiological stress responses to changes in various behaviors (Maestripieri et al. 1992). However, some researchers have reservations about these connections (MacDougall-Shackleton et al. 2019—see details below). Due to this, many ecotourism-focused researchers attempt to measure either physiological stress, potential behavioral stress, or both. For example, Tibetan macaques (*Macaca thibetana*) at Mt. Huangshan, China, display behaviors that may be related to stress more when tourists are present and in response to certain tourist behaviors (Matheson et al. 2006). In addition, howler monkeys (*Alouatta palliata*) in Belize show signs of physiological stress as numbers of tourists increase (Aguilar-Melo et al. 2013). Also, Barbary macaques (*Macaca sylvanus*) scratch more when exposed to large groups of tourists and have higher fecal glucocorticoids after aggressive tourist/macaque interactions (Maréchal et al. 2011). In the present study, we aim to test the general hypothesis that levels of potential stress-related behaviors in three groups of wild, habituated Sulawesi crested macaques (*Macaca nigra; yaki in the local Manadonese dialect)* in Tangkoko Nature Reserve (TNR), NE Sulawesi, Indonesia, are related to aspects of tourism.

4.1.2 Habituation of Primates for Tourism

The local citizens of Batu Putih, a village on the edge of TNR, live alongside multiple *Macaca nigra* social groups. When tourism spread across the globe, the economic value of wildlife became clear. Tourism inside TNR was first formally documented in 1978. Despite exposure to tourists for nearly two decades, Kinnaird and O'Brien found in 1996 that small groups of unknown humans caused *M. nigra* to flee, a potential behavioral response to stress. In order to benefit from tourists flocking to the North Eastern Sulawesi region (Muller 1992; National Resources Management Project 1993), local guides needed macaque groups to stay stationary and on the ground for extended periods of time. The most effective way to achieve this without force was through habituation.

Habituation is a reduction in responses over time as sensory stimuli are perceived as neither adverse nor beneficial (Bejder et al. 2009). It enables an organism to filter out excess environmental stimuli, allowing it to focus on factors critical to its survival. Conversely, stimuli that are perceived as dangerous elicit physiological stress-related responses, which, in excess, can be detrimental to health and/or fitness (Moberg 2000). The ability to recognize situations that pose no threat, and thereby avoid unnecessary physiological stress-related responses, is likely to enhance chances for survival and reproduction. Hence, to reduce possible harm to wild subjects, ensure maintenance of natural behaviors, and facilitate observation, researchers and ecotourism operators seek to habituate target groups (Goodall 1986). In the early days of wild primate observation, a widely used method for "accelerated habituation" was through food provisioning (see Knight 2009; Yamagiwa 2011 for review). Over time, it became clear that provisioning primates as a means for habituation was problematic. Human-directed aggression and crop raiding increased in areas where accelerated habituation was employed (Knight 2009; Yamagiwa 2011). These two behaviors can be detrimental to both nonhuman primates and the people who live around them. Conversely, long-term habituation entails repeated exposure to neutral interactions with observers over time (Tutin and Fernandez 1991; however, see Hanson and Riley 2017, for review of habitation between humans and primates as an intrasubjective process). Researchers often assume that habituation has been achieved when their subjects tolerate their presence, i.e., "the relatively persistent waning of a response as a result of repeated stimulation…" (Hinde 1970).

This definition has led to the assumption that tolerance equals habituation, and habituation equals harmless levels of physiological stress-related responses. Site operators have taken a cue from researchers and use similar methods and criteria to habituate targeted primate groups in an effort to make them more accessible to the growing number of tourists (Johns 1996).

However, habituation is an ongoing behavioral process, requiring considerable long-term scrutiny of both behavioral and biological responses to perceived disturbances (Bejder et al. 2009). As opposed to habituation, what we see more often at tourism sites is apparent "tolerance" of animals to anthropogenic presence (see Blumstein 2016 for review). Indeed, some studies have shown that at several primate field sites, overt primate behavioral changes to human presence decrease quickly (after several months), but less noticeable responses (subtle behaviors or cortisol levels) decrease over a much longer period (Jack et al. 2008; McDougall 2012; Williamson and Feistner 2011). Thus, it may be inaccurate to assume primates are fully habituated and are not experiencing maladaptive levels of physiological stress-related responses. Additionally, many factors are likely to play into the ways in which animals respond to environmental challenges and potential stressors like human disturbance. For example, individuals may respond differently based on their age, sex, dominance status, or personality (Balasubramaniam et al. 2020b; Coleman 2012; Martin and Réale 2008; Sapolsky 2005). Moreover, different characteristics of a potential stressor, such as numbers of tourists or familiar vs. unfamiliar humans, may induce different behavioral responses (Frid and Dill 2002) that may also vary with ecological conditions, including food availability or rainfall (Sheriff et al. 2011). Finally, apparent behavioral tolerance may present in the form of general behavioral inhibition in response to signs of human presence nearby. Such inhibition may not be obvious to observers but may accompany a physiological stress response and/or represent a mild form of threat assessment or avoidance, e.g., vigilance or avoidance of detection. Untangling all these factors is important in any examination of potential stress-related behavior in wild primate groups.

4.1.3 Primate Stress-Related Behaviors

Researchers have identified a number of specific behaviors in primates in laboratory studies that correlate with levels of physiological stress indicators, including glucocorticoids (Maestripieri et al. 1992). These behaviors are used as proxies for the strength of an organism's response to stress and will be referred to throughout this chapter as "stress-related behaviors" or SRBs. These behaviors, although indirect indicators, allow researchers an easy, inexpensive, noninvasive means, to detect minute-to-minute stress-related responses in individuals when hormonal analysis is not possible. The two most commonly studied SRBs are displacement activities: self-scratching and self-grooming (Troisi 2002) both of which increase when captive long-tailed macaques (*Macaca fascicularis*) are injected with an anxiogenic drug meant to induce anxiety (Schino et al. 1996). These behaviors have also been shown to be associated with stressful situations in the wild. For example, intragroup aggression has been shown to increase rates of scratching in wild brown lemurs (*Eulemur fulvus*) (Palagi and Norscia 2011). Additionally, a multifactor study of self-directed behaviors in free-ranging Japanese macaques (*Macaca fuscata fuscata*) provided evidence that self-grooming can act as a displacement activity; it increased in the presence of social uncertainty (Duboscq et al. 2016). However, this has not consistently been the case in primate studies and, in some instances, scratching either decreased or showed no change in the presence of a potential stressor (Maréchal et al. 2016; Ulyan et al. 2006). Other explorations of scratching as an SRB in wild primates suggest that some scratching may simply be due to environmental conditions in the wild, such as increased numbers of biting insects (Duboscq et al. 2016) or ambient temperature and humidity (Ventura et al. 2005). Additional explanations have also come to light, focusing instead on the function of scratching as opposed to its cause. Higham et al. (2009) posited that scratching may be a behavioral coping mechanism, helping ameliorate physiological stress responses. While a study by Whitehouse et al. (2017) suggested that scratching (what they qualify as an observable stress behavior) in primates is adaptive because of its presumed ability to reduce escalated aggression, thereby improving social cohesion. Laméris et al. (2020) came to a similar conclusion when exploring scratching as a behavioral contagion in captive Bornean orangutans (*Pongo pygmaeus*).

Due to the conflicting results surrounding displacement activities such as self-grooming and self-scratching, researchers measure additional behaviors that may suggest increased stress, such as increases in aggression, changes to rates of vocalizations, and decreases in both sexual and affiliative behaviors. For example, Clarke et al. (1996) examined the relationships between aggression, immunological, and hormonal responses associated with social change in two groups of captive rhesus monkeys (*Macaca mulatta*). They found a consistent relationship between aggression and physiological stress indicators in the study group. Specifically, both non-contact aggression and cortisol levels increased during the first 24 hours after an introduction of a new member. Also, in a seminal study, Rowell and Hinde (1963) examined *M. mulatta* behavioral response to a potential threat, a human wearing a "scary" mask. They found that the presence of the mask greatly reduced the frequency of calling (a mix of contact and food calls), which were present in all three other conditions: control, food, and familiar human. A more recent study by Pérez-Galicia et al. (2017) found a decrease in vocalizations in the presence of humans in a group of spider monkeys (*Ateles geoffroyi*) maintained at an island in Mexico. In addition, Mitchell et al. (1991) examined the behavior of zoo-housed, golden-bellied mangabeys (*Cercocebus chrysogaster*). When mangabey groups housed in an enclosure experiencing a moderate number of daily visitors were moved into an enclosure experiencing a low number of daily visitors (a switch from a presumably stressful situation to a less stressful one), sexual behaviors, grooming, and play increased. Also, Chamove et al. (1988) found that 15 species of captive primates showed significantly less affiliative behavior in the presence of visitors (presumably a perceived stressor). Wild primates show similar reactions. For example, proboscis monkey (*Nasalis larvatus)* infants significantly decreased their frequency of social behaviors as numbers of tourists increased, a potential behavioral response that may have been related to stress (Leasor and Macgregor 2014). However, Marty et al. (2019) linked an increase in social behaviors with an increase in SRBs in a group of long-tailed macaques (*Macaca fascicularis)* residing at a site with a high level of anthropogenic impact. While not directly linked to human presence, there is the possibility that increasing social behaviors in times of stress can act as a coping mechanism (e.g., social buffering hypothesis). Conversely, other studies suggest that individuals may use affiliative behavior in more complex ways than just an increase or decrease to cope with potentially stressful situations. For example, Wittig et al. (2008) found that when wild female chacma baboons experienced a stressful situation, as potentially indicated by increases in cortisol, those who reduced their grooming network to a few strong relationships, without necessarily changing their overall grooming rates, displayed greater reductions in cortisol levels than those who maintained a more diverse network made up of weaker relationships. Thus, the size of the social network is important and grooming rates do not always correlate directly with stress. Additionally, Balasubramaniam et al. (2020a) found that semi-urban bonnet macaques (*Macaca radiata*) who spend more time monitoring humans decreased their time spent grooming conspecifics. However, affiliative behaviors with short durations, i.e., lip-smacking, showed no change, indicating that context and behavior have a complex relationship.

4.1.4 Confounds in Measuring Stress-Related Behaviors

Given these complications to using a single SRB, we used a variety of presumed indicators to examine possible associations between macaque stress and aspects of tourism. We define them as “presumed indicators” since changes in these behaviors might have other explanations. For example, macaques may be distracted by tourists and not stressed per se. Distraction might be indicated by an inhibition in behavior, including the self-directed behaviors (SDBs) defined as self-scratching and self-grooming. To complicate matters further, many internal and external factors may change the way a primate responds to a stressor. Given this, controlling multiple possible confounding factors is vital when examining possible stress-related responses to tourism. For example, individual rank influences the way a primate responds to a stressor behaviorally (see review Cavigelli and Caruso 2015). Additionally, a recent study by Woods et al. (2019) assessed visitor-directed aggression in zoo-housed Japanese macaques *(Macaca fuscata*) by rank and found that low-ranking individuals displayed more frequent aggression toward visitors. Considering male primates specifically, the particular reproductive season (Fichtel et al. 2007), the number of fertile females present (Engelhardt et al. 2011, unpublished), or the number actively in a consortship (Bergman et al. 2005) could influence levels of aggression, affiliative behaviors, sexual behaviors, and/or cortisol. Also, male dispersal from their natal group into a new group can influence levels of cortisol, which, in turn, may influence SRBs (*Macaca nigra:* Marty et al. 2017a). In female primates, the number of young infants present in the group could influence levels of aggression. In many species, mothers display heightened aggression in defense of their young (see review Hahn-Holbrook et al. 2011). Alternatively, levels of conspecific affiliation may also shift, as seen in wild ring-tailed lemurs (*Lemur catta*), where affiliative behaviors between adult females increase in the presence of young infants (Nakamichi and Koyama 2000). Additionally, individual reproductive state may influence the way females respond behaviorally due to the physiological links between reproductive hormones and cortisol (Weingrill et al. 2003). Food availability is an external factor of concern. Cortisol is generated to metabolize stored energy reserves when food is scarce (Sapolsky et al. 2000). As such, low food availability is sometimes, but not always, associated with higher fecal glucocorticoid levels (Foley et al. 2001; Pride 2005; Sapolsky 1986). For example, Behie et al. (2010) found a complex relationship between overall food availability, fruit consumption, and cortisol levels in two groups of mantled howlers (*Alouatta palliata*). Specifically, when fruit availability was low, cortisol levels increased. The supposition is that when fruit availability is low, monkeys eat less fruit and therefore obtain less sugar. Indeed, prior literature suggests that the lack of fruit (sugar) may be particularly responsible for adaptive increases in cortisol levels as it increases glucose mobilization (Muller and Wrangham 2004). Whether such diet-related changes in cortisol levels are related to changes in SRBs is unclear. Nevertheless, recognizing the importance of untangling as many factors as possible, we collected data on and controlled for all of these factors during statistical analysis.

4.1.5 Tourism inside Tangkoko Nature Reserve

There is an urgent need to understand the factors, both natural and anthropogenic, that contribute to *Macaca nigra* fitness. The International Union for Conservation of Nature (IUCN 2022) lists *M. nigra* as critically endangered and rates their conservation as a high priority. The study site, Tangkoko Nature Reserve (TNR) is a popular ecotourist location and home to the last remaining, viable population of *M. nigra* (see review Danish et al. 2017).

Previous research has examined the influence of tourism on crested macaque behavior inside the park. As mentioned above, Kinnaird and O'Brien (1996) found that exposure of one macaque group to seven or more tourists often produced fleeing. Additionally, two smaller groups that were less exposed to tourism had either a lower or zero tolerance for tourists. However, this occurred before full habituation (enabling daily, year-round researcher visits) of the macaques. Over a decade later, Paulsen (2009) found that, between two consecutive summers, crested macaque aggressive behaviors increased in frequency and escalated more quickly in the presence of tourists.

In the present study, we tested the hypothesis that levels of stress-related behaviors (SRBs) are associated with aspects of tourism in three habituated groups of wild *M. nigra* in TNR named R1, R2, and PB1. These groups represent a natural experiment, each exposed to different intensities of tourism (R2 = frequently, R1 = moderately, and PB1 = rarely/research only). All three groups have had similar exposure to researchers associated with the Macaca Nigra Project (MNP) for about 15 years. Although the number of researchers in each group varied by day (and was recorded daily), it was limited to 6 for R2 and R1 and 4 for PB1. The two tourism groups (R1 and R2) have been exposed to tourists (and accompanying guides) for about three decades. Additionally, while one group rarely encounters tourists, tourist groups are sometimes loud, and large groups of them can be heard from a great distance. Due to this, we asked not only about the possible effects of the presence of tourists within study groups, but also about possible effects of tourists in the reserve when outside and away from the study groups. MNP is careful to limit the number of researchers in each group, but they have no control over the number of tourists or guides. The TNR tour guide rules (unpublished but distributed, 2015) state that no guide can bring more than four tourists. However, DB and team frequently saw one guide with ten or more tourists or two guides with four or fewer tourists. To control for this in our analysis, we kept track of the number of guides and numbers of tourists, in each macaque group per day.

TNR borders Batu Putih gardens and village homes, both of which present enticing food sources. The macaque social groups were also exposed to guarding of crops when they ventured just outside the park boundaries (generally involving TNR personnel making whooping noises, chasing, or setting off fireworks) with the same variation in frequency as exposure to tourists (R2 = frequently, R1 = moderately, and PB1 = rarely). Due to this, we also recorded daily crop guarding events and avoided recording data during and within 30 min of a crop guarding event in an effort to untangle behavioral responses to tourism from behavioral responses to crop guarding.

4.2 Specific Hypotheses and Predictions

4.2.1 Hypothesis 1: Possible Effects of Tourists in the Forest

We predicted that **(H1)** if exposure to tourists influences the display of SRBs even when tourists are not present within the group, then **(P1)** we will find significant differences in SRBs that are related to levels of exposure to tourism. Specifically, (**H1a**) if groups with more tourist exposure experience more stress than groups with less tourist exposure, then **(P1a**) R2 and R1 will display significantly higher rates of aggression and SDBs and significantly lower rates of sociality and vocalizations than PB1. Also, (**H1b**) if temporal variation in tourist presence in the forest is associated with SRBs, then **(P1b)** we will find significantly higher rates of aggression and SDBs and significantly lower rates of sociality and vocalizations in those months with more tourists in the forest. Moreover, (**H1c**) if the monthly numbers of tourists in each group affect individual groups differently, then (**P1c**) there will be a significant interaction effect between group and numbers of tourists per month; i.e., group responses will be related to their levels of exposure to tourists. Alternatively, (**H1d**) if exposure to tourists in the forest inhibits behavior, then (**P1d**) we will find lower rates of all SRBs in months with many tourists.

4.2.2 Hypothesis 2: Possible Effects of Presence Vs Absence of Tourists within Groups

We predicted that (**H2)** if levels of direct exposure to tourists in the group influence the display of SRBs, then (**P2**) we will find significant differences in SRBs related to their direct exposure to tourists. Specifically, (**H2a**) if the presence of tourists in a focal session is stressful, then (**P2a**) groups will display significantly higher rates of aggression and SDBs and significantly lower rates of sociality and vocalizations during focal sessions with tourists as opposed to those in their absence. Additionally, (**H2b**) if tourist presence itself is stressful, (**P2b**) then groups will display significantly higher rates of aggression and SDBs and significantly lower rates of sociality and vocalizations in those focal sessions that have higher numbers of tourists than those sessions with lower numbers. Also, (**H2c**) if regular exposure to tourists is stressful, then (**P2c**) groups will display significantly higher rates of aggression and SDBs and significantly lower rates of sociality and vocalizations on those days that have higher numbers of tourists over the course of the day than on days with lower numbers. And (**H2d**) if groups with more tourist exposure experience more stress than groups with less tourist exposure, then (**P2d**) R2 will display significantly higher rates of aggression and SDBs and significantly lower rates of sociality and vocalizations than R1. Moreover, (**H2e**) if tourist presence during a focal affects individual groups differently, then (**P2e**) there will be a significant interaction effect between group and tourist presence vs. absence; i.e., group responses will be related to their levels of exposure to tourists. Alternatively, (**H2f**) if the presence of tourists inhibits behavior, then (**P2f**) we will find lower rates of all SRBs when tourists are present than absent, in the group with more tourists (R2), and/or on days with many tourists.

4.2.3 Hypothesis 3: Possible Effects of Researchers and Guides

Finally, we predicted that (**H3**) if macaques respond with stress to familiar (as opposed to unfamiliar) humans, then (**P3a**) we will see increases in SRBs when more researchers are present in the group each day than less, and (**P3b**) we will see increases in SRBs when more guides are present in the group each day than less.

4.3 Materials and Methods

4.3.1 Study Site and Species

Tangkoko Nature Reserve is a location of robust megadiversity (Rhee et al. 2004) that once claimed the highest number of endemic species in any protected area on the island of Sulawesi (MacKinnon and MacKinnon 1980), including *M. nigra.* The population of *M. nigra* in this 8867-hectare nature preserve is most likely the only viable and natural remaining population in the wild (Palacios et al. 2011; Riley 2010; Supriatna and Andayani 2008). The most recent survey indicates that one half of the park supports a population of 1951 or 44.9 individuals per km^2 (Palacios et al. 2011). Another recent survey assessed 61.5 individuals/km^2 (Kyes et al. 2012), which comes close to population numbers of 76 individuals/km^2 from almost 30 years ago (Sugardjito et al. 1989). However, the assessment by Kyes et al. (2012) focused only on the tourism (615 ha) and protected areas (3835 ha), representing approximately one-half of the park.

M. nigra utilizes a variety of habitats including lowland primary forests, areas of cultivation surrounded by primary and secondary forests, actively logged forests, and dense human habitation and agriculture (O'Brien and Kinnaird 1997; Rosenbaum et al. 1998). Crested macaques are diurnal and semi-terrestrial and spend 59% of their day traveling, foraging, and feeding with the remaining time spent resting and socializing (O'Brien and Kinnaird 1997). Their diet consists primarily of fruit, supplemented with other plant parts as well as invertebrate and vertebrate prey. They live in large multi-male, multi-female groups (O'Brien and Kinnaird 1997), and their social organization is female philopatric and female bonded, with males dispersing at sexual maturity and secondarily at intervals throughout adulthood (Duboscq et al. 2013; Marty et al. 2017b; Reed et al. 1997). Coresident adult males are usually not related and primarily use avoidance when interacting, perhaps indicative of tension due to risky reproductive competition (Tyrrell et al. 2020). Females are more egalitarian and utilize connections with higher ranking males to ensure better foraging options and protection from harassment by lower ranking males (Duboscq et al. 2013; Kinnaird and O'Brien 1996; Reed et al. 1997). They are nonseasonal breeders, with a tendency toward birth peaks between January and May (Engelhardt and Perwitasari-Farajallah 2008).

4.3.2 Tourism

TNR is not a new tourism site. Several macaque social groups have been subjected to daily visits from unfamiliar humans (tourists) for over four decades (MacKinnon and MacKinnon 1980). In the 90s, the popularity of TNR as an ecotourist location experienced a surge (Kinnaird and O'Brien 1996) and has continued to gain in popularity annually (Natalia Kandyoh: Tangkoko Ticket Master, personal communication, 2016). Park rules change frequently, but in general, tourists are required to remain with a guide while in Tangkoko, unless they are going to the beach. However, it is important to note that the macaques can and do frequent the beach. Tourist groups range in size from 2 to 25 individuals, are not required to remain on trails (i.e., they can walk up to a group of monkeys), and can remain in the forest for several hours (from dawn until dusk). Both local and international tourists are allowed to camp inside the park on the beach side. In general, during the low tourist (rainy) season, our research indicated that macaque groups are exposed to an average of 2 tourist groups per day, while during the high tourist (dry) season they can be exposed to an average of 7 groups per day, often more than one at a time. Interacting with the macaques is prohibited, and flash photography is discouraged; however, guides rarely enforce these rules. Additionally, when habituation first began with foreign researchers in the late 70's, food (specifically bananas) was the most commonly used tactic in TNR to increase macaque comfort around unfamiliar humans (Petrus Takasaheng & Alfons Wodi: Tangkoko Guides, personal communication, 2016). While discouraged today, feeding by guides and rangers continues unimpeded (Bertrand, D., personal observation). In addition, the macaques have access to tourist food from garbage bins in the park itself.

4.3.3 Field Methods and Subjects

Data collection took place over 14 months (10/2014–01/2016) within groups R2, R1, and PB1, located inside TNR: group R2 (22–23 adults who experienced research, and frequent tourism), group R1 (40–42 adults who experienced research and moderate tourism), and group PB1 (22–23 adults who experienced research only). Due to their ranging patterns, PB1 encountered tourists on rare occasions. However, either MNP researchers would inform tour guides that the group was restricted, and the tourists would continue through the forest, or the tour guides themselves would recognize the group and direct tourists around them.

We collected behavioral data from 33 adult *M. nigra* (age ≥ 7 years, 15 males and 18 females). MNP categorizes (1) individual adult macaque age as young, middle, or old, (2) female rank (using David's Scores) as either low, middle, or high, and (3) male rank numerically (using Elo ratings), with the number 1 representing the highest ranking male. We obtained both rank and age data from MNP in November 2014, before the start of data collection. In order to ensure that the sample of macaques was comparable across groups, we selected six females from each group with corresponding ages and ranks. They were as follows: three young females—one high ranking, one middle ranking, and one low ranking—and three middle-aged females—one high ranking, one middle ranking, and one low ranking. Female *M. nigra* ranks within their respective groups are linear and generally stable over time (Duboscq et al. 2013). Thus, we anticipated no major changes. Males were selected differently. In R1, we chose six males, four categorized as middle aged and two categorized as old. These macaques were spread out evenly across their linear ranks (1, 3, 5, 6, 9, 10). However, it was not possible to match them with specific males in R2 and PB1 as they had less than six males each. Thus, our selected males from these groups were a mix of ages, ranked 1–5 and 1–4 respectively. Male rank is highly asymmetrical and linear; changes were anticipated (Marty et al. 2017a, b). All ranks were verified and corrected when necessary, by myself, before data analysis using Elo ratings for males and David's Scores for females. Behaviors used for this can be found on Table 4.1.

Table 4.1 *Macaca nigra* behaviors analyzed (All behaviors use standard definitions as defined by the Macaca Nigra Project)

Behavior	Event (When necessary, definitions were adapted from instructions to MNP staff and researchers)
Affiliative—within interval sampling	
Body contact	To stand/sit/lie in contact of another individual more than 5 s. The touch can be with any part of the body.
Social groom	To clean the fur/skin of another one. Hairs are brushed and parted using the hands, while particles are picked up by the hands/mouth.
Ventral embrace	To put arms around another individual often with affiliative facial expressions, face to face with potential ventro-ventral contacts—Unidirectional or bidirectional.
Lateral embrace	To stand side by side but facing in opposite directions, each individual drapes an arm over the other's hips or waist, sometimes both partners inspect the other's genitals—Bidirectional.
Hug	To pass one or both hands/arms around the body of another (multiple combination).
Expressive run	To run away and approach again back and forth another individual while doing affiliative facial expressions and/or repeated soft grunts. Often occurs between females with infants or more rarely between two males involved in affiliative interactions (like mounts and genital grasp).
Play	To engage in relaxed and more or less exuberant patterns including loping gait, running, climbing, swinging, rolling, sliding, jumping, walking on hands, bouncing, pirouetting, toppling, uncoordinated moving, stamping, support shaking, handling, dragging, or throwing an object. Any of these patterns may appear in solitary or social play.
Mock bite	To softly bite the body of a social partner in an action of play or copulation. Occurs as well between males engaged in friendly interactions.
Play face	Relaxed open mouth display. To have teeth bared and the mouth open. It signals the performer's desire to play or to interact friendly.
Genital grasp	Between males or male and juvenile—To grab each other's genitals.
Mount	Between same sex—To climb ventro-dorsally upon a standing partner. The mounter may or may not grip the legs of the partner.
Unknown affiliation	Any affiliative interactions (if not seen in detail); includes but not limited to when focal is hugged, when focal is mounted and when focal is genital grasped.
Aggressive—continuous sampling (* indicates behavior used in rank determination)	
Half-open mouth	To slightly open the mouth with corners drawn back, the lower lip may be retracted and the teeth are partly visible. This display is accompanied by staring. Could also be accompanied by a rattle.

(continued)

Table 4.1 (continued)

Behavior	Event (When necessary, definitions were adapted from instructions to MNP staff and researchers)
Open mouth bared teeth	To open the mouth more or less widely. The teeth and the gums could be exposed. It is accompanied by a threat or a scream. It is used as an attack or in a counterattack.
Jaw movement	To thrust head forward, and the lower jaw is moved up and down rapidly and rhythmically. Could be accompanied by scalp retraction and/or ears flatten and/or a low threat vocalization.
Stare	To look intensively to another individual. Could be accompanied by the half-open mouth. Acts as a mild threat.
*Chase	To run after another individual on more than 2 m to make it run away and/or bite/hit/grab it.
*Bite	To bite another individual.
*Hit	To hit another individual with any limb
*Grab	To catch and hold in a hand a bunch of fur of another one to retain it.
*Push	To push with hand or body to make an individual move away.
Support shake	To stand on a branch or whatever and shake or jump on this support. It is a “show off” behavior.
*Lunge	To make a short run (< 2 m) or a jump toward an individual (warning that could lead to an aggressive behavior.)
Stamp	To make a short run or a jump and finally stand stiff on its forelimb. May be follow by yawning/staring or the half-open mouth display (context of tension or play or aggression to attract attention).
Harassment	Several individuals threat, chase, bite, hit, and grab together against another one. Often during intergroup encounter, one individual of one group is harassed by many of the other. It is also the case when an individual comes to disturb friendly or aggressively a copulative pair.
*Scream	Noisy scream vocalization.
*Flight	To run away in response to another’s approach/aggression.
*Crouch	To press body on the ground, 4 limbs flexed in response to another’s approach/aggression.
*Protection seeking	An individual threatened or attacked by another approachesand contacts a third individual.
Enlisting	To look several times at a particular individual close by or around to call for support while involved in an aggressive interaction.
Unknown aggression	Any aggressive interaction (if not seen in detail).
Ignore	To stay without reacting when an individual approaches or directs affiliative/aggressive behaviors.
Glance/look away	To avoid making eye contact when an individual interacts or attempts to.
Sexual—continuous sampling	
Sexual present	A female raises or orients the hindquarters toward a male at proximity and may turn the head toward it. Could be accompanied by looking at the male or grasping his genitals. It signals the female’s motivation to mate.
Sexual parade	A female presents toward a male several times, passing repeatedly in front of him.
Sexual mount	A male climbs ventrodorsally upon a standing female. He may or may not grip the legs of the female.

(continued)

Table 4.1 (continued)

Behavior	Event (When necessary, definitions were adapted from instructions to MNP staff and researchers)
Mate	A male mounts and introduces his penis in the female's vagina and thrusts. Record when both the male and female are focal.
Silent bared-teeth jaw movement	To vertically retract lips, exposing the teeth, and the lower jaw is moved rhythmically and silently. It is typical of a male when a female approaches or passes by or presents toward the male.
Reaching back	A female grasps the fur, leg, arm, face, or genital of the mating male
Ejaculation	To pulse the anus during mating. Usually occurs only after a series of matings.
Vocalization—continuous sampling	
Contact/lost calls	Louder when far away and/or losing visual contact with the group. If two or more calls are emitted within 5 s of each other, only one "vs" should be recorded.
Alarm call	Short and loud, repeated. Signals a danger (python, people).
Female copulation call	(Repetitive) Call given after copulation, can be loud or low.
Male copulation call	Shrieking vocalization by the male during copulation. Often two parts, but record even if only one part is heard.
Loud call	Adult male vocalization occurs in various contexts (e.g., aggression and mating).
Self-directed behavior—continuous sampling	
Self-groom	To clean its one fur.
Self-scratch	To rake the skin repeatedly using fingers of hands or feet.

In summary, DB and team followed 6 males and 6 females from R1, 5 males and 6 females from R2, and 4 males and 6 females from PB1. There were only two male migrations during the data collection period: one subadult male from R2 into R1 in September 2015 and one unknown subadult male into R1 in mid-November 2015. Because migrants were all subadults, they were not added as focal subjects. We lost one male from PB1 early into the study period (only collected 8 min from him). There was no male to replace him. Additionally, we lost three females at varying time points. From R2, one preselected female died shortly before data collection began. From R1, we lost one female shortly after the study began (we only collected 10 min of data from her) and another female a few weeks later (62 minutes collected from her). For all three, we selected a new female focal of comparable age and rank.

4.3.4 Ethics and Research Permits

The protocols used in the study were approved by the Institutional Animal Care and Use Committee of the University at Buffalo (#ANTO2082N). All protocols adhered to strict ethical standards for wild primate research that were designed in consultation with Macaca Nigra Project and the Institut Pertanian Bogor to comply with the legal requirements of Indonesia. All research and physiological sample collection/

shipment permits were obtained and renewed on the appropriate timelines from Balai Konservasi Sumber Daya Alam (Conservation of Natural Resources in North Sulawesi), Kementerian Riset dan Teknologi (Indonesian Ministry of Research & Technology), and Direktorat Jenderal Konservasi Sumber Daya Alam dan Ekosistem (Indonesian Directorate General of Nature Resources and Ecosystem Conservation).

4.3.5 Behavioral Data Collection

A team of six assistants and DB collected behavioral data related to the macaques' responses to tourist presence and characteristics. The assistants comprised three recent college graduates from the United States, and three recent college graduates from Indonesia. We conducted two-minute focal follows to record rates of behavioral stress indicators (SRBs): self-directed behaviors (SDBs, including self-scratching and self-grooming), aggression, vocalizations, and sexual behaviors. These short focal sessions had proven effective in preliminary research. The macaque groups tended to spread out, with tourists moving in between smaller subgroups. Therefore, tourists may have only been within 10 m of a focal monkey for a few minutes at a time. Additionally, a large portion of R1 and R2's home range was comprised of secondary forest with thick scrub, making longer focal sessions difficult.

We also used 1/0 sampling to record the occurrence of affiliative behaviors within the two-minute focal session (see Table 4.1 for complete list and definitions). Each focal session began with a point time sample to record the presence and absence of tourists as well as tourist characteristics (number of, gender, age, and foreign/domestic distinction). All members of the team participated in interobserver reliability testing for identity recognition and the full ethogram of behaviors. For identity recognition, long-term observers (Research Manager and permanent field assistants) were the standards. No statistical test was used. We were tested until we could identify 100% of macaques in each group. For behavioral testing, DB was the standard and we used Cohen's kappa coefficient as our reliability measure. All team members reached reliability levels of at least Kappa 0.96.

The order of focal sessions was randomly assigned for each day of the week, before the week's observations, using an online randomization generator. If two assistants were in the same group, the focal subjects were split equally between them. Thus, an observer was responsible for between 5 and 12 focal macaques on any given day. Each focal subject had at least 30 min between each of their focal sessions. We achieved this easily because, regardless of how many focal subjects were assigned to an observer; it often took several minutes to find the next focal subject on the list. If a focal subject was not found within 15 min, the observer moved to the next subject down the list. Additionally, if a focal subject was lost before the 1-min 45-s mark of the 2-min focal session and the observer did not find their lost focal subject within 5 min, the focal session was deleted. See Table 4.2 for total focal hours collected per individual and group in each condition.

Table 4.2 Number of focal hours and focal sessions analyzed

Focal hours for Hypothesis 1									Focal hours for Hypothesis 2 and Hypothesis 3							
Group R1			Group R2			Group PB1			Group R1			Group R2			Group PB1	
Macaque ID	Hours	Sessions	Macaque ID	Hours	Sessions	Macaque ID	Hours	Sessions	Macaque ID	Hours	Sessions	Macaque ID	Hours	Sessions	Macaque ID	Hours and sessions
Ak	17.69	531	An	24.69	741	Aa†	14.07	422	Ak	20.73	622	An	31.2	937	Aa†	N/A
Cu†	15.06	452	Fd†	24.56	737	Ba†	15.05	452	Cu†	17.12	514	Fd†	30.6	918	Ba†	N/A
Ej	15.02	451	Id†	24.30	729	Bp†	15.51	465	Ej	17.19	516	Id†	30.0	900	Bp†	N/A
Fu†	18.28	548	Od†	23.07	692	Cp†	15.08	452	Fu†	21.22	636	Od†	29.1	873	Cp†	N/A
Gs†	16.84	505	Qd†	22.42	672	Fm	15.52	466	Gs†	18.92	568	Qd†	27.2	817	Fm	N/A
Hs†	17.69	531	Rm	20.16	605	Ql	7.55	226	Hs†	19.56	587	Rm	24.5	734	Ql	N/A
Kn	18.46	554	Rn	24.02	721	Rp†	14.30	429	Kn	21.74	652	Rn	31.7	950	Rp†	N/A
Ll	17.70	531	Td†	24.24	727	Uk	14.67	440	Ll	20.91	627	Td†	30.3	910	Uk	N/A
Mm	18.04	541	Tl	25.18	755	Ul	15.29	459	Mm	21.41	642	Tl	34.2	1025	Ul	N/A
Nu†	17.21	516	Wj	26.53	796	Up†	16.39	492	Nu†	20.35	610	Wj	34.4	1031	Up†	N/A
Om	16.24	487	Zd†	24.75	743				Om	18.42	553	Zd†	30.5	916		
Qs†	15.75	473							Qs†	17.86	536					
Total male	100.83	3025	Total male	120.49	3615	Total male	53.04	1591	Total male	99.66	2990	Total male	155.99	4680	Total male = N/A	
Total female	103.14	3094	Total female	143.43	4303	Total female	90.4	2712	Total female	135.76	4073	Total female	177.7	5331	Total female = N/A	
Total group	203.97	6119	Total group	263.92	7918	Total group	143.33	4300	Total group	235.42	7063	Total group	333.69	10,011	Total group = N/A	
Mean ± SE hours per focal subject = 18.53 ± 1.055									Mean ± SE hours per focal subject = 24.74 ± 1.293							
Total hours for hypothesis 1 = 611.33									Total hours for hypothesis 2 and hypothesis 3 = 569.11							
Total hours analyzed = 739.5																
† denotes female									† denotes female							

Table 4.3 Fruit availability index at Tangkoko Nature Reserve 2014–2015

$\sum_1$ = Sum of log food scores	N = # trees measured	Log mean food abundance = $\sum_1/N$
$\sum_2$ = sum of plots	X = # of trees sampled in each species in all plots	Mean density = $\sum_2/X$
FAI = $(\sum/N)*(\sum_2/X)$		

Several variables were tabulated after data collection was complete. We calculated the number of tourists in the park each month by summing the number of tourists present in all groups each day. While it is possible that some tourists were “double counted’ and that others never visited a group, e.g., beach goers or tarsier tourists, these problems were probably minimal because groups were often far apart from each other and it was unlikely that tourists visited both on the same day. In addition, when the groups were close together, no focal sessions were recorded because it was considered to be an “intergroup encounter,” thus potentially biasing the measurement of stress-related responses to tourists. We calculated the number of tourists in each group each day by summing the actual number of tourists present in the group from the moment the macaques came down out of their sleeping tree to the moment they were up in their sleeping tree. We calculated the number of guides each day by summing the numbers of guides present in each group from the moment the macaques came down out of their sleeping tree to the moment they were up in their sleeping tree (Table 4.3).

Finally, as we were concerned about high-energy food sources and their potential effect on physiological stress responses, we calculated a fruit availability index (FAI). We calculated this with phenology data collected by Macaca Nigra Project staff using a method designed by Dr. Oliver Schulke and a formula modified from a food availability index derived by Sari (2013). It included all known fruit species foraged by the monkeys except mango trees (spp *Mangifera*), which were not included in the phenology dataset. Furthermore, the measurement of the productivity of coconut trees (*Cocos nucifera*) was problematic partly because the total number of coconut trees was unavailable. Hence, it was not possible to calculate their density, a critical component in the FAI formula. Alternatively, coconut fruits were removed from the formal FAI calculations and instead marked as either present or absent during a data collection month. Recognizing the importance of coconuts as a high-energy food source, we transformed our FAI to a mean rank measure to include the potential use of coconuts during a given month. The formula used in the present study was as follows: FAI = (Sum of log food scores/# trees measured) / (# of trees sampled in each species in all plots/20 plots) = $(\sum_1/N)*(\sum_2/X)$.

4.3.6 Data Analysis

We tested the predictions of H1–H3 using general linear mixed model (GLMM) analysis from the LME4 package version 1.1–12 in R 3.3.3 [Release Version 1.68 (7328)]. One set of models was run for H1 (Model 1), and another set (Model 2) was run for H2 and H3. Separate models were run for males and females and for each SRB. Our unit of analysis was the individual focal session. Each stress-related behavior was entered as the response variable in a separate model. SRBs analyzed were rates of aggression, rates of self-directed behaviors (SDBs: self-scratching and self-grooming), presence or absence of affiliative behaviors, rates of sexual behaviors, and rates of vocalizations. See Table 4.4 for a list of specific model factors.

Before each GLMM model was built, collinearity among variables was tested to ensure all fixed and random effects were not highly correlated with one another. All fixed and random factors had VIF factors below 3. After this, data were explored with qnorm functions to identify the appropriate distribution for GLMM family selection. All response variables indicated Poisson distributions, except for affiliative behaviors, which were collected using 1/0 sampling, indicating a binomial distribution. All behavioral responses explored with Poisson GLMM models included code to offset by the total time, in seconds, of each focal session, providing true rates of behavior.

For each type of analysis, the first model run was always the null (consisting of the response variable, the control factor of fruit availability, and the random factor of macaque ID). The second model run was the full factor model. When evaluating differences between full models and null models, we applied Bonferroni corrections separately to each set of five models within each dataset (those for H1 for males, H1 for females, H2 for males, and H2 for females) by setting a critical level of $0.05/5 = 0.01$ to each model. All full models were significantly different from the null, indicating that one or more fixed effects in the full model were associated with variation in the response factor. Otherwise, criteria for significance were $p \leq 0.05$. All models were checked for overdispersion by testing if the model deviation was larger than the mean. If a model was significantly overdispersed, this indicated that there was greater variability (statistical dispersion) in a dataset than would be expected based on a given Poisson statistical. In these cases, we corrected overdispersion by creating an additional random intercept for each focal session (Elston et al. 2001).

When running GLMM models on behavioral data that fit a Poisson model, it was not always possible to retain this Poisson family due to either a lack of convergence or eigenvalue errors. Convergence errors indicate that the model has too many factors for its sample size and cannot be fit. Eigenvalue errors indicate that one of the variables has a range that is skewed far from the response variable range. In order to correct for convergence errors, we increased GLMM model iterations. If convergence errors did not disappear with the third iteration increase, the response variable was collapsed into a binomial form. In order to correct for eigenvalue errors, it was necessary to rescale one or more continuous variables to a smaller range by converting the data to standard scores and then rescaling to a specified mean. If eigenvalue errors did not disappear, the model would not proceed and we collapsed the response variable data into a binomial form.

Table 4.4 Description of model factors

Factor name	Definition	Present in model:
Group	Social group (R1, R2, or PB1)	1 and 2
Rank/Elo	Dominance rank of focal subject	1 and 2
Monthly_Tourist	Sum of the number of tourists present each month in the forest	1 and 2
fai_rank	Fruit availability index transformed into a ranking system	1 and 2
T-Den	Number of tourists present during focal session	2
Type	Type of focal session, (tourists present vs. free from any anthropogenic condition other than researchers	2
Num_of_Tourists	Daily number of tourists in the focal subject's group	2
Number_of_guides	Daily number of guides present in the focal subject's group	2
Num_of_Researchers	Daily number of researchers present in the focal subject's group	1 and 2
Repro_state.Coll	Individual female macaque reproductive state	1 and 2
Sum.CG.Events	Sum of numbers of days in a month that had one or more crop guarding event	1 and 2
CropGuard	Occurrence of daily crop guarding in the focal subject's group (yes/no)	1 and 2
Fertile	Number of fertile females present each month	1 and 2
Infant	Number of young infants present each month	1 and 2
Monkey[a]	Focal subject ID	1 and 2
Helper	Random intercept to control for over dispersion, if present	1 and 2
C.Con_Agg	Rate of conspecific-directed aggression	1 and 2
Vocal	Rate of vocalizations	1 and 2
NewAffiliative	Occurrence of affiliative behavior in a focal session (yes/no)	1 and 2
SDB.Stress.Binom	Occurrence of stress behaviors in a focal session (yes/no)	1 and 2
SDB.Stress	Rate of stress behaviors	1 and 2
Sexual_Beh	Rate of sexual behaviors	1 and 2

[a] Each model included the focal's ID as a random factor

4.4 Results

4.4.1 Possible Effects of Tourists in the Forest

Results for H1, which involved examining behavior when no tourists were present in the group (but were present in the forest), are shown in Table 4.5. In **Prediction 1a,** we asked if PB1, as the research only group, displayed lower rates of SRBs than R1 and R2. Consistent with this prediction, PB1 females scratched less than R2 females ($Z = -1.99$, $p < 0.0463$). However, PB1 males scratched more than R1 males ($Z = 3.76$, $p = 0.046$), and PB1 females affiliated less than R2 females ($Z = -2.48$, $p = 0.013$), a finding contrary to our prediction.

In **Prediction1b,** we asked whether the groups may have been affected by the presence of varying numbers of tourists in different months in the park. We found the following main effects: Males vocalized less ($Z = -1.98$, $p = 0.047$), showed fewer SDBs ($Z = -5.91$, $p < 0.001$), and displayed fewer sexual behaviors ($Z = -2.68$, $p = 0.007$) in months with greater numbers of tourists. In addition, females aggressed less ($Z = -2.53$, $p = 0.011$), vocalized less ($Z = -4.64$, $p < 0.001$), showed fewer SDBs ($Z = -4.42$, $p < 0.001$), and displayed fewer sexual behaviors ($Z = -2.95$, $p = 0.003$) in months with greater numbers of tourists. These results did not support the prediction that individuals would display more stress-related behaviors in months with more tourists (**P1b**), but they were consistent with the prediction that (**P1d**) greater numbers of tourists may inhibit macaque behavior.

Finally, we asked **(P1c)** whether responses to numbers of tourists per month varied by group or whether all groups responded in a similar manner. Given main effects suggestive of general inhibition of SRBs, we predicted that PB1 would have responded more slowly or less intensely to numbers of tourists each month than R1 and R2. The results for vocalizations were consistent with these predictions as indicated by significant interaction effects for group by monthly tourist numbers. As monthly numbers of tourists increased, R2 males decreased their rate of vocalization faster than either PB1 or R1 (R2 vs. PB1: $Z = -2.86$, $p = 0.004$; R2 vs. R1: $Z = -2.77$, $p = 0.006$), R1 and R2 females decreased rates of vocalizations faster than PB1 (R1 vs. PB1: $Z = -2.28$, $p = 0.022$; R2 vs PB1: $Z = -4.40$, $p < 0.001$), and R2 females decreased rates of vocalizations faster than R1 ($Z = -1.93$, $p = 0.049$). However, results for other measures were generally in the opposite direction from predicted. PB1 females decreased rates of aggression faster than R1 ($Z = -2.51$, $p = 0.012$); PB1 females decreased rates of sexual behaviors faster than either R1 or R2 (PB1 vs. R1:$Z = -2.11$, $p = 0.035$; PB1 vs. R2: $Z = -1.96$, $p = 0.048$); PB1 males decreased their rates of SDBs faster than either R1 or R2 (PB1 vs R1:$Z = -4.45$, $p < 0.001$; PB1 vs. R2: $Z = -3.23$, $p = 0.001$), and R2 decreased their rates of SDBs faster than R1 ($Z = -2.13$, $p = 0.033$); PB1 and R2 females decreased rates of SDBs faster than R1 females (PB1 vs. R1:$Z = -4.27$, $p < 0.001$; R2 vs. R1: $Z = -3.45$, $p < 0.001$). R1 females were the only ones to increase their scratching rate.

Table 4.5 Model 1—responses to tourists in the forest

	Dependent Variables									
Fixed effects	Aggression		Vocalizations		Affiliative		SDBs		Sexual	
Males	SD	z	SD	z	SD	z	SD	z	SD	z
# Tourists/mo	0.01	0.65	0.01	**−1.98***	0.01	−0.75	0.01	**−5.91*****	0.02	**−2.68****
Group	Chisq = 3.07		Chisq = 2.68		Chisq = 2.74		**Chisq = 13.49****		Chisq = 1.10	
PB1 vs R1	0.24	−1.57	0.23	−1.21	0.22	1.68	0.08	**3.76*****	0.49	1.06
PB1 vs R2	0.24	−1.66	0.24	−1.62	0.23	0.71	0.08	0.33	0.50	0.79
R1 vs R2	0.21	−0.14	0.23	−0.51	0.20	−1.05	0.07	**−3.74****	0.45	−0.27
Group x no. tourists/mo	Chisq = 0.62		**Chisq = 11.93****		Chisq = 1.97		**Chisq = 19.82*****		Chisq = 3.66	
PB1 vs R1	0.01	0.76	0.02	0.88	0.01	−1.12	0.01	**−4.45*****	0.02	−1.67
PB1 vs R2	0.01	0.52	0.01	**2.86****	0.01	−0.22	0.01	**−3.23****	0.02	−0.71
R1 vs R2	0.01	−0.01	0.01	**2.77****	0.01	1.26	0.01	**2.13***	0.02	1.51
No. researchers	0.02	−1.58	0.02	−1.60	0.02	0.39	0.01	0.87	0.03	0.50
Rank	0.05	0.85	0.05	1.19	0.06	0.85	0.02	−0.45	0.09	−1.33
Fertile females	0.03	**3.35*****	0.03	0.66	0.04	−1.46	0.01	**−2.02****	0.05	1.19
# crop guard events/mo	0.00	−0.58	0.00	**2.28***	0.00	−1.33	0.01	**−5.76*****	0.01	**4.03*****
Fruit availability index rank	0.02	−1.20	0.02	**4.13*****	0.02	1.86	0.01	**13.87*****	0.03	**7.36*****
Females	**SD**	**z**	**SD**	**z**	**SD**	**z**	**SD**	**z**	**SD**	**z**
# Tourists/mo	0.01	**−2.53***	0.01	**−4.64*****	0.01	−1.15	0.01	**−4.42*****	0.04	**−2.95****
Group	Chisq = 1.56		Chisq = 3.65		**Chisq = 6.19***		Chisq = 4.26		Chisq = 2.34	
PB1 vs R1	0.20	−0.05	0.21	−1.21	0.13	−0.90	0.08	−0.57	0.76	1.54
PB1 vs R2	0.20	−1.03	0.23	−1.83	0.14	**−2.48***	0.09	**−1.99***	0.79	1.30
R1 vs R2	0.18	−1.13	0.20	−0.75	0.12	−1.84	0.08	−1.66	0.71	0.22
Group x no. tourists/mo	**Chisq = 6.95***		**Chisq = 49.66*****		Chisq = 1.02		**Chisq = 20.42*****		Chisq = 5.00	
PB1 vs R1	0.01	**−2.51***	0.01	**2.28****	0.02	−0.85	0.01	**−4.27*****	0.04	**−2.11***
PB1 vs R2	0.01	1−.20	0.01	**4.43*****	0.02	−0.09	0.01	−1.60	0.04	**−1.96***
R1 vs R2	0.01	1.86	0.01	**1.93***	0.02	0.92	0.01	**3.45*****	0.03	0.69

(continued)

Table 4.5 (continued)

	Dependent Variables									
Fixed effects	Aggression		Vocalizations		Affiliative		SDBs		Sexual	
Males	SD	z	SD	z	SD	z	SD	z	SD	z
No. researchers	0.02	1.93	0.02	1.27	0.02	−1.76	0.01	**−1.98***	0.05	0.68
Rank	Chisq 3.28		Chisq = 1.00		**Chisq = 6.23***		Chisq = 3.64		Chisq = 2.63	
High vs middle	0.15	−1.88	0.12	−0.98	0.09	1.37	0.09	−1.92	0.61	0.87
High vs low	0.20	−1.19	0.17	−0.27	0.12	−1.43	0.07	−0.42	0.82	1.76
Middle vs low	0.18	−0.19	0.15	−0.49	0.12	**2.66****	0.08	1.76	0.77	−1.18
Reproductive state	**Chisq = 70.31*****		**Chisq = 18.98*****		Chisq = 1.18		Chisq = 1.46		**Chisq = 226.01*****	
Cycling vs lactating	0.08	**−4.99*****	0.07	−1.96	0.06	0.24	0.02	−0.11	0.44	**9.09*****
Cycling vs pregnant	0.09	**2.09***	0.06	**−2.67****	0.06	−0.70	0.03	−1.18	0.17	**7.06*****
Pregnant vs lactating	0.07	**−8.14*****	0.05	0.70	0.06	1.05	0.03	0.88	0.45	**6.01*****
# of infants	0.02	−0.02	0.02	**−1.99***	0.01	−1.80	0.01	**−8.33*****	0.05	1.07
# crop guard events/mo	0.00	−0.47	0.00	**5.55*****	0.01	−1.38	0.01	**−3.94*****	0.01	−1.46
Fruit availability index rank	0.02	1.53	0.01	0.34	0.01	**4.36*****	0.01	**11.71*****	0.05	**3.71*****

*** p ≦0.001, ** p ≦0.01, * p ≦0.05

4.4.2 *Presence Vs Absence of Tourists*

Results for **Hypothesis 2**, which involved examining behavior of the two tourism groups, are shown in Table 4.6. In **Prediction 2a,** we asked if tourist presence vs. absence in a focal session influenced the display of SRBs. We found that that females displayed less affiliation (Z = −2.15, p = 0.031) and more aggression (Z = 3.33, p = 0.001) during focal sessions in which tourists were present as opposed to absent. In addition, males aggressed more (Z = 2.60, p = 0.009). These results support the prediction that macaques responded to the presence of tourists during a focal session with increases in some stress-related behavior (**P2a**) but not with general inhibition of behavior (**P2f**). There were no other measures with significant differences. In **(P2b),** we examined whether the number of tourists present in each focal session was related to the display of SRBs. Only females displayed any variation in SRBs with numbers of tourists within the group. When more tourists were present, they had higher rates of SDBs (Z = 3.75, p < 0.001). In **Prediction 2c,** we asked if the total numbers of tourists present in the group each day were related to the display of SRBs. Both males and females displayed significantly lower rates of SDBs when the number of tourists present each day were higher (males: Z = −3.01, p = 0.003; females: Z = −4.69, p < 0.001). Additionally, females displayed significantly lower rates of vocalizations when the numbers of tourists present each day were higher (Z = −2.86, p = 0.004). Although these results were consistent with the idea that tourists within groups inhibited scratching and vocalizing, results for no other SRBs reached statistical significance. As such, these results are not consistent with predictions for stress (**P2c**) and represent weak evidence of inhibition (**P2f**). In (**P2d**), we predicted that the group that experienced more direct exposure to tourists would display more behavioral stress indicators. However, we found no significant differences in SRBs between the two groups. Finally, **P2e** asked whether the two groups differed in their responses to the presence vs absence of tourists or whether both groups responded in a similar manner. Although R2 was exposed to tourists more frequently than R1, there were no significant interactions between tourist presence vs. absence and group for any SRB.

4.4.3 *Researchers and Guides*

Finally, results for **Hypothesis 3** (using data from Model 2) in which we asked whether the daily numbers of researchers (**P3a**) and guides (**P3b**) present in each group were related to the display of SRBs are shown in Table 4.6. We found that males displayed less aggression when a greater number of researchers were present (Z = −2.24, p = 0.025). However, females displayed higher rates of aggression (Z = 2.91, p = 0.001) and lower rates of SDBs (Z = −3.55, p < 0.001) when a greater number of researchers were present. No other measures varied significantly with numbers of researchers. As such, these results do not represent strong evidence for

Table 4.6 Model 2 and Model 3—responses to tourists in social groups R1 and R2

	Dependent variables									
Fixed effects	Aggression		Vocalizations		Affiliative		SDBs		Sexual	
Males	SD	z	SD	z	SD	z	SD	z	SD	z
Tourist yes/no during focal	0.14	**2.60****	0.19	−0.68	0.19	0.48	0.06	−0.23	0.22	0.88
# Tourists/mo	0.01	−0.10	0.01	**−3.73*****	0.01	−1.20	0.00	**−10.40*****	0.02	−1.48
# Tourists/day	0.03	0.93	0.03	1.12	0.01	−0.83	0.01	**−3.01****	0.46	−0.27
# Of tourists in each focal	0.01	0.25	0.02	−1.13	0.01	−0.04	0.00	1.18	0.03	−1.22
Group R1 vs group R2	0.23	0.54	0.22	0.97	0.20	−0.34	0.15	−1.29	0.39	0.81
Group x tourist yes/no	Chisq = 1.57		Chisq = 0.80		Chisq = 0.14		Chisq = 0.57		Chisq = 0.10	
R1 vs R2	0.13	1.25	0.18	0.89	0.17	−0.37	0.06	−0.78	0.22	0.31
# Of guides	0.07	−1.20	0.10	0.21	0.10	**−2.00***	0.03	**−2.24***	0.11	1.91
No. researchers	0.03	**−2.24***	0.03	−1.63	0.03	1.46	0.01	0.69	0.04	0.73
Rank	0.07	−0.66	0.07	1.65	0.07	0.92	0.02	0.64	0.12	0.34
Fertile females	0.04	1.53	0.04	1.20	0.05	−1.41	0.01	−1.02	0.06	0.04
Crop guard yes/no during day	0.07	1.52	0.08	**2.66****	0.08	0.57	0.03	**3.59***	0.12	1.44
Fruit availability index rank	0.02	0.23	0.02	**2.93****	0.02	1.58	0.01	**11.56*****	0.04	**7.62*****
Females	**SD**	**z**	**SD**	**z**	**SD**	**z**	**SD**	**z**	**SD**	**z**
Tourist yes/no during focal	0.18	**3.33*****	0.17	0.77	0.16	**−2.15***	0.07	−1.85	0.55	0.86
# Tourists/mo	0.01	**−2.44***	0.01	**−4.54*****	0.01	**−2.90***	0.00	**−8.79*****	0.03	**−3.62****
# Tourists/day	0.03	1.61	0.03	**−2.86****	0.01	−0.69	0.01	**−4.69****	0.09	−1.60
# Of tourists in each focal	0.01	0.68	0.01	0.45	0.01	−1.13	0.00	**3.75*****	0.03	−0.16
Group R1 vs group R2	0.17	−1.14	0.21	0.67	0.11	−1.89	0.10	−1.47	0.73	−0.10
Group x tourist yes/no	Chisq =0.52		Chisq = 2.35		Chisq = 3.19		Chisq = 0.01		Chisq = 0.01	
R1 vs R2	0.16	0.72	0.15	1.32	0.14	−1.78	0.07	−0.11	0.46	0.05
# Of guides	0.11	**−3.01****	0.09	−0.83	0.08	−0.38	0.04	0.08	0.30	−0.93

No. researchers	0.03	**2.91****	0.03	1.38	0.02	−0.07	0.01	**−3.55*****	0.07	0.57
Rank	**Chisq = 8.02***		Chisq = 1.44		Chisq = 3.20		Chisq = 1.05		Chisq = 2.77	
High vs middle	0.30	−1.63	0.40	0.31	0.20	−1.22	0.14	−1.03	1.62	1.69
High vs low	0.16	**−3.25****	0.21	−1.10	0.10	1.20	0.07	−0.43	0.72	0.15
Middle vs low	0.29	−0.92	0.38	−0.93	0.19	1.83	0.13	0.83	1.55	−1.69
Reproductive state	**Chisq = 55.12*****		**Chisq = 40.56*****		Chisq = 0.49		Chisq = 5.15		**Chisq = 84.08*****	
Cycling vs lactating	0.12	**−4.52*****	0.12	−0.63	0.09	−0.55	0.03	0.99	0.76	**5.56*****
Cycling vs pregnant	0.12	1.61	0.11	**−3.15****	0.09	−0.69	0.03	−1.73	0.22	**5.77*****
Pregnant vs lactating	0.10	**−2.73*****	0.10	**2.67****	0.08	0.12	0.04	**2.18***	0.75	**3.92*****
# Of infants	0.02	−1.67	0.02	**2.28***	0.02	−0.30	0.01	**−3.65*****	0.06	1.55
Crop guard yes/no during day	0.08	**−2.14***	0.07	−0.50	0.06	**−2.28***	0.03	**3.21****	0.18	**−2.73****
Fruit availability index rank	0.02	1.19	0.02	1.74	0.02	**3.13****	0.01	**8.77*****	0.07	2.97**

*** $p \leqq 0.001$, ** $p \leqq 0.01$, * $p \leqq 0.05$

either increases in stress-related behavior or behavioral inhibition. In contrast, we found limited evidence of behavioral inhibition related to numbers of guides: Males displayed affiliative behaviors in fewer focal sessions ($Z = -2.00$, $p = 0.045$) and lower rates of SDBs ($Z = -2.24$, $p = 0.025$) when a greater number of guides were present. Females displayed lower rates of aggression when a greater number of guides were present ($Z = -3.02$, $p = 0.002$).

4.5 Discussion

This study aimed to test the general hypothesis that levels of stress-related behaviors in groups of wild *M. nigra* in Tangkoko Nature Reserve (TNR), NE Sulawesi, Indonesia, are related to aspects of tourism. We collected data from three habituated groups with varying levels of exposure to tourism. Overall, our results suggest that wild crested macaques are behaviorally inhibited when more tourists are present in the forest but not present within groups. In addition, they show signs of both inhibition and increases in stress-related behaviors when tourists are present directly in social groups. We tentatively suggest that these responses can be viewed within the framework of typical responses of primates to perceived predators posing varying degrees of risk. Below, we develop this argument in greater detail.

In those months where greater numbers of tourists were present in the forest, we saw, in general, an inhibition of macaque behaviors: Males vocalized less and displayed fewer sexual behaviors and SDBs, and females vocalized less, aggressed less, and showed fewer SDBs. In addition, several measures suggested that degrees of inhibition in the three groups were associated with their levels of direct exposure to tourists. PB1, the group that was exposed to tourists the least, appeared to react more strongly than the other two groups to increased numbers of tourists in the forest each month; PB1 generally showed more intense decreases in aggression, sexual behavior, and SDBs than the other groups. This raises the hypothesis that PB1's relative lack of direct exposure to tourists may have led to more intense behavioral inhibition to their presence in the forest. Vocalizations, however, showed the opposite association with PB1 decreasing its vocalization rates less intensely in response to numbers of tourist in the forest. As such, this finding and those for differences between the two tourist groups complicate this interpretation. Both males and females in the more highly exposed R2 group showed more intense decreases in vocalizations than those in R1. Of note, while our vocalization measures analyzed here included contact calls, long calls, and sexual calls, contact and long calls made about 96% of the total vocalizations.

In contrast, when examining behavior when tourists were present vs. absent within groups during focal sessions, we found some behavioral differences consistent with the idea that direct exposure to tourists is associated with immediate increases in stress-related behavior. Both sexes displayed significantly higher rates of aggression toward conspecifics, and females displayed significantly lower rates of sociality when tourists were present within the group. In addition, when more tourists were present, females displayed higher rates of SDBs. At the same time, other results suggested some evidence of inhibition of behavior when the total numbers of tourists present in the group each day were high; both males and females displayed lower rates of SDBs and females vocalized less, raising the possibility that large numbers tourists over the course of a day may moderate responses somewhat to tourists within groups. This possibility could be tested in the future by looking at changes in responses to tourist groups on a given day as numbers of tourists accumulate over the course of the day. It may also be useful to look at the timing of tourist visits as well as their numbers. On some days, the groups of tourists waited for the macaques at their sleeping trees until they awoke, while on other days the macaques would not encounter any tourists until late afternoon. These changes in visiting tourist patterns not only introduce uncertainty, but may also alter baseline tolerance levels.

Evidence of both behavioral inhibition and increases in typical stress-related behaviors such as increased aggression and SDBs requires a careful examination of the context surrounding each type of response. Inhibition of behavior in one context with an increase in aggression in another may seem surprising, but may be possible to interpret within a framework of responsiveness to different levels of perceived risk to predators, as described by Roelofs (2017). Roelofs posited that as predator threat levels increase, animals move from freezing to fight-or-flight responses. As such, we tentatively suggest that unfamiliar humans trigger mild predator avoidance responses in wild crested macaques and further that they may respond with different behaviors to different levels of perceived risk. These responses appear to have three stages: inhibition, increased SDBs, and increased aggression toward/flight from perceived predators.

While large hawks and pythons are known predators of this population, the macaques' top predator is currently humans through poaching and timber harvesting (Hilser et al. 2013; Supriatna et al. 2020). When the threat of a poacher becomes immediate, macaques typically alarm call and flee into high trees (Diswal Takasaheng: Tangkoko Guide, personal communication, 2015). Due to their experience with poachers, wild crested macaques in Tangkoko may also view unfamiliar tourists as threatening to some extent. Unfamiliar tourists resemble poachers in some respects but not others. Whereas researchers and guides visit groups frequently (with researchers wearing distinctive shirts), poachers and unfamiliar tourists visit rarely and do not wear distinctive clothing. Additionally, only poachers typically bring dogs. Thus, unfamiliar humans likely represent the unknown and add uncertainty to the context.

While there is still much to be learned about predator avoidance/defense in primates, some similarities in predator avoidance behaviors are found across primate species, including vigilance (Stanford 2002). Vigilance is generally defined as a visual scanning of the area (Beauchamp 2015), but it is also typically accompanied by a "freezing," or a general inhibition of behavior (Roelofs 2017). Moreover, behaviors considered to indicate "anxiety," such as scratching, tend to decrease in the presence of behaviors considered to indicate "fear" such as freezing (Barros et al. 2004) As predator presence becomes more evident or proximate, primates may shift to a 2nd stage of predator defense including clumping of individuals (e.g., females gathering infants and moving closer to males), alarm calling (Stanford 2002), and in some cases may increase rates of self-scratching (Palagi and Norscia 2011). However, scratching does not follow this pattern in all primate species. Neal and Caine (2016) found that captive common marmosets (*Callithrix jacchus*) decreased their rates of self-scratching during a predator simulation (and after alarm calling began). While this appears to contradict our addition of self-scratching as part of stage two in a three-stage response to predation, Troisi et al. (1991) suggest that self-scratching increases only during moderate—as opposed to low or high—levels of anxiety. Levels of tolerance in various contexts likely determine when an individual experiences low, medium, or high levels of anxiety. Although there is little information about subtle behavioral responses at this second stage, they are likely to be marked by motivational conflict, i.e., uncertainty about whether to stay put to avoid detection, flee, or confront the predator. Given that displacement behaviors, including fear-related aggression toward conspecifics and SDBs, tend to be displayed during motivational conflict (Blurton Jones 1968; Van Lawick-Goodall: cited in Hinde 1974; Maestripieri et al. 1992), the increases in both types of response are likely to be seen when macaques are confronted by uncertainty. For example, tourists directly present within a group are likely perceived as riskier than when tourists are outside the group and easier to avoid. Maréchal et al. (2016) also showed this pattern of displacement behavior in habituated Barbary macaques, which appeared to depend on a trade-off between perceived risks vs. potential benefits (provisioned food) from tourists. This example has an important parallel to *M. nigra* in TNR for whom access to food from tourists, guides, garbage, and nearby crops could incentivize them to stay in this area despite heightened stress. It may also be that such behaviors help to mitigate/cope with the physiological effects of fear and stress (Higham et al. 2009). The final (3rd) stage of predation avoidance/defense usually includes either increased aggression toward or fleeing from predators (Beauchamp 2015).

In the present study, we found that when tourists were evident in the forest, but not within study groups, macaques in all three social groups showed evidence of inhibition of a wide range of behavior: affiliative, aggressive, sexual, and self-directed, responses that collectively could be considered partial or mild freezing responses. As such, it is possible that as unfamiliar tourists are heard in the forest, macaques practice vigilance to monitor the whereabouts of tourists and avoid detection. When tourists appear within groups, we found evidence of both inhibitions, for example, on days when large numbers of tourists appeared, and of motivational uncertainty in relation to risk; SDBs and conspecific aggression were both increased, consistent with a second stage of response to predators. Finally, although we did not record any instances of tourist-directed aggression or fleeing (stage 3 behavior), PB1 occasionally still fled from tourists approaching their group and, on rare occasions, macaques (in R2) attacked humans within groups without clear provocation (personal observation, 2015). Further exploration of these rare instances would be valuable.

Comparing our findings with those of earlier researchers of this population, it appears that as tourism in the park has grown over the years, *M. nigra* behavioral responses have changed. In the early days of observation and tourism in this population, macaques in the study groups typically fled from observers (MacKinnon and MacKinnon 1980) and later from groups of tourists larger than seven (Kinnaird and O'Brien 1996). During the current study, they only rarely fled when confronted with tourists or directed aggression toward tourists within groups. Overall, the results of this study suggest that primate groups exposed to tourism, even for decades, may not fully habituate to tourists. Although the groups now generally appear to tolerate the presence of large groups of tourists in the forest and within groups, our results challenge a common assumption among primate researchers and conservationists that, when long-term exposure to presumed benign anthropogenic influences such as tourism leads to apparent tolerance, habituation is complete. Rather, it appears as though tourists may still be perceived as sources of risk by such populations, inducing mild responses similar to predator avoidance. Whether these risk perceptions also lead to potentially harmful physiological stress responses, and their accompanying fitness effects, is not clear. However, several studies have shown evidence of increased glucocorticoids in response to tourists in other primates (Rangel-Negrín et al. 2014; Shutt et al. 2014; Cañadas Santiago et al. 2019).

Why males and females responded differently to familiar humans (researchers and tourist guides) is difficult to interpret. Males displayed less aggression when a greater number of researchers were present, while females displayed more aggression. Additionally, males displayed less affiliation when more guides were present, while females displayed less aggression. It may be that males and females differ in their risk perceptions of familiar humans based on their individual appearances or behavior rather than on (or in addition to) their numbers. There is also the possibility that, at least in the case of females, the presence of a greater number of guides reduces the potential threat of tourists. The differences between responses to researchers vs. guides may be twofold. First, researchers spend all day with macaque groups—from sunrise to sunset. This is a long period of time to have humans following and watching the group. While males may see them as a protective, familiar element, females (especially those with young infants) may not find their watchful presence as comforting. Secondly, MNP researchers undergo training and habituation to groups for several months before collecting data. Tourist behavior is not as controlled, and they lack the knowledge and understanding of primate behavior to make their presence less stressful. Notably, some MNP permanent research assistants also serve as guides. While not analyzed here, we recorded researcher IDs and guide names. With a deeper analysis, we may be able to uncover specific characteristics of familiar humans that play a role in the macaques' response, e.g. differences in gender, experience, and roles (researcher vs guide). Regardless, our results here urge caution for all primate field sites to review their protocols for number of researchers present at one time. If indeed researcher presence impacts primate behavior, this could be detrimental to group cohesion. Possible ways to mitigate these behavioral shifts could involve periodic assessments of monkey responses to researcher numbers and characteristics and could be paired with ongoing training.

While the results of this study appear to be reasonably consistent with a predator avoidance framework, they involved only a moderate number of subjects. Moreover, while the amount of time some subjects were observed in the presence of tourists was relatively short, the number of independent focal sessions themselves was high due to the short nature (~2 min) of each focal session. Future studies are needed with larger samples to validate them. Additionally, a more accurate measure of tourist numbers and attributes in the forest would be ideal. As of late 2016, TNR promoted their Ticket Master to full time and requested she keeps a daily log of tourist names, which guides attend which tourist groups, and total tourist counts. This includes tourists who only go to the beach, without intending to visit macaques or tarsiers specifically. Additionally, it would be useful to measure distances between focal macaques and tourist groups in order to examine responses to tourists at varying distances.

Future studies would also benefit by examining changes in behavior over time within a day. Is there a threshold number of tourists present at the same time that triggers a strong predator response, similar to the early Kinnaird and O'Brien study that uncovered a limit of seven? Additionally, it is possible that certain tourist characteristics (e.g., gender, age, national vs international) illicit stronger responses than others. Do the macaques respond more strongly to certain stimuli presented by some tourists, perhaps stimuli most closely associated with predation, or do they respond uniformly to all unfamiliar humans? While we know that many primates recognize different species of predators and respond adaptively with different behaviors (Cheney and Seyfarth 1981), evidence has shown that most primates have evolved more general predator avoidance tactics to specific stimuli, (e.g., unexpected sounds, moving shadows overhead, unexpected visual changes to the environment). Therefore, any organism that provides such stimuli is likely to elicit a predator avoidance/defensive response (see review Schel and Zuberbühler 2009).

Overall, it is important to note that SRBs themselves may be the result of a variety of causes. Untangling one direct cause is unlikely. However, it may be possible to demonstrate their relationship to stress physiology by complimenting these behavioral results with data on physiological responses to tourism, while also keeping in mind that glucocorticoids, including cortisol, are not only activated during periods of stress, but also play a primary function in energy mobilization and have numerous pleiotropic effects in vertebrates (MacDougall-Shackleton et al. 2019). Such a study should ideally relate behavioral and physiological responses to fitness-related measures, e.g., infant mortality rates, given that stress is, at its core, an adaptive response (Moberg 2000) that only becomes maladaptive under particular conditions (Sapolsky 1992). Similar to Beale and Monaghan (2004), all of the above could be combined into a comprehensive model of perceived predation risk and used as a framework for understanding the effects of tourist disturbance. Such a model should ultimately better enable conservation biologists and site managers to identify aspects of tourism and primate management in need of modification and thus bring tourism operations and human/animal conflict management practices in better alignment with their intended goals.

While a more comprehensive study is warranted, we tentatively recommend certain policies related to *M. nigra* viewing in Tangkoko. Both the numbers of guides and tourists should be limited. Guides should be encouraged to bring small groups incrementally into the forest. Additionally, it would be beneficial for paid guides or park rangers to monitor the beach area, as it is frequently visited by all three macaque groups. When tourists are in the forest, silence should be encouraged and feeding/touching discouraged. Tangkoko recently opened a "Visitor Center" at the entrance of the park. Paid staff could orient tourists on proper behavior around macaques, such as no eye contact, no rapid movements, and no touching the flora. Our recommendations leave room for additional job creation for the local village, providing new areas to educate visitors, protect the forest as a whole, and showcase this critically endangered species.

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