

Interactions between human and long-tailed macaque (*Macaca fascicularis*) in the context of crop feeding in Mauritius

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Interactions between human and long-tailed macaque (*Macaca fascicularis*) in the context of crop feeding in Mauritius



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Abstract

Interactions between human and long-tailed macaque (*Macaca fascicularis*) in the context of crop feeding in Mauritius

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January 2025, Behavioral Biology Unit

Human-wildlife coexistence in agro–forestry systems often presents significant challenges. In Mauritius, the long-tailed macaque (*Macaca fascicularis*) – an introduced species – is reported as a serious crop pest by local farmers, but its crop feeding behavior remains poorly studied. Yet, understanding this behavior is essential for developing effective and sustainable mitigation strategies.

We used a combination of camera trap data, crop damage assessments, and phenological surveys to quantify macaque activity in agricultural fields. More specifically, we investigated the effects of spatial, temporal and demographic factors on the frequency and duration of macaques' visits to the fields (hereafter referred to as Crop Feeding Events or CFEs). Secondly, we sought to identify which key parameters of CFEs - including frequency, duration and number of individuals - could best predict the amount of damage caused to crops. A questionnaire survey was then conducted to examine farmers' perceptions and attitudes toward macaques. Across six study sites, we recorded a total of 776 macaque videos, including 193 CFEs. Our results showed that crop feeding group sizes were generally small, with an average CFE duration of 14 minutes. Distinct macaque activity patterns were observed between sugarcane and vegetable crops, likely influenced by human presence. We found that demographic composition of the group was a key factor, with CFEs duration increasing with the size of the group and the proportion of adults. Spatial factors, such as the proportions of surrounding forest and farmland, were associated with shorter feeding events. Our research identified the frequency of CFEs as the primary parameter for determining crop loss, although the number of individuals and the duration of CFEs were also important secondary factors. Our questionnaire revealed that, overall, farmers' perceptions of macaques were predominantly negative and influenced by socio-cultural variables. Farmers with a Hindu affiliation, those who were younger or had a higher level of education expressed greater tolerance toward macaques compared to other respondents. The majority of respondents (81%) also reported a marked increase in macaque visits to their crops over the past ten years.

This exploratory study offers valuable insights into the patterns and drivers of crop feeding by Mauritian macaques, which could inform future mitigation strategies. We recommend prioritizing deterrence methods aimed at reducing the frequency of CFEs. For example, the use of 'buffer' crops or enhancing the perception of risk in fields by employing guards or dogs, when feasible—techniques that remain underutilized for macaques in Mauritius. We also suggest that key CFE parameters could serve as useful measures for testing the effectiveness of future macaque deterrents. Additionally, our results underscore the importance of considering the human dimension, as poorly designed interventions may unintentionally exacerbate tensions among religious or social groups. These socio-cultural factors must be taken into account to ensure that mitigation efforts are not only effective but also socially sustainable.

Résumé

Interactions entre les humains et les macaques à longue queue (*Macaca fascicularis*) dans le contexte du nourrissage dans les cultures à l'île Maurice.

Salomé Vallet Adams | Promoteur.trices : Raphael Reinegger (UBristol) & Fany Brotcorne (ULiege)
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La coexistence entre l'homme et la faune dans les systèmes agroforestiers est souvent source de grands défis. À l'île Maurice, les agriculteurs locaux signalent le macaque à longue queue (*Macaca fascicularis*), une espèce introduite, comme un ravageur majeur pour les cultures, mais les détails de son comportement alimentaire sont peu connus. Pourtant, la compréhension de ce comportement est essentielle pour mettre en place des stratégies de mitigation efficaces et durables.

Nous avons utilisé une combinaison de données issues de pièges photographiques, d'évaluations des dommages causés aux cultures et de relevés phénologiques pour quantifier l'activité des macaques dans les champs agricoles. Plus précisément, nous avons étudié l'effet des facteurs spatiaux, temporels et démographiques sur la fréquence et la durée des visites des macaques dans les champs (désignées ci-après comme *CFEs* pour *Crop Feeding Events*). Dans un second temps, nous avons cherché à identifier quels paramètres clés des CFEs — parmi la fréquence, la durée et le nombre d'individus — pouvaient le mieux prédire la quantité de dommages causés aux cultures. Une enquête par questionnaire a été menée ultérieurement pour examiner les perceptions et les attitudes des planteur.se.s à l'égard des macaques. Sur les six sites d'étude, nous avons enregistré un total de 776 vidéos de macaques, dont 193 CFEs. Nos résultats ont montré que les groupes se nourrissant dans les cultures étaient généralement de petite taille, avec des visites d'une durée moyenne de 14 minutes. Des schémas d'activité distincts ont été observés entre les champs de cannes à sucre et de légumes, probablement influencés par la présence humaine. Nous avons trouvé que la composition démographique du groupe était un facteur clé, la durée des événements de nourrissage augmentant avec la taille du groupe et la proportion d'adultes. À l'inverse, les facteurs spatiaux, tels que la proportion de forêts et de terres agricoles environnantes, étaient associés à des visites plus courtes. Notre recherche a identifié la fréquence des événements de nourrissage comme le paramètre principal pour déterminer les pertes de récoltes, bien que le nombre d'individus et la durée des CFEs soient également des facteurs secondaires importants. Notre questionnaire a révélé que, dans l'ensemble, la perception des planteur.se.s envers les macaques était majoritairement négative et influencée par des variables socioculturelles. Les personnes de religion hindoue, celles étant plus jeunes ou ayant un niveau d'éducation plus élevé ont exprimé une tolérance accrue à l'égard des macaques. La majorité des répondant.e.s (81 %) ont également signalé une nette augmentation du nombre de CFEs dans leurs cultures au cours des dix dernières années.

Dans l'ensemble, cette étude exploratoire permet d'apporter des informations sur les comportements alimentaires des macaques mauriciens, pouvant guider de futures stratégies de mitigation. Nous recommandons de prioriser des méthodes de dissuasion réduisant la fréquence des CFEs, comme l'utilisation de cultures « tampons » ou l'emploi de gardes ou de chiens, - des techniques qui restent sous-utilisées à Maurice. Les paramètres clés des CFEs pourraient servir d'indicateurs afin d'évaluer l'efficacité des techniques de dissuasion. Enfin, nos résultats soulignent l'importance de considérer la dimension humaine, car des interventions mal conçues peuvent exacerber les tensions sociales ou religieuses, rendant nécessaire l'intégration de ces facteurs pour des solutions non seulement efficaces mais également socialement durables.

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Table of abbreviations

AIC Akaike Information Criterion

AICc Corrected Akaike Information Criterion

CT Camera Trap

CFE Crop Feeding Event

DBH Diameter at Breast Height

GLM Generalized Linear Model

GLMM Generalized Linear Mixed Model

HWC Human-Wildlife Conflict

HWCC Human-Wildlife Conflict and Coexistence

HWI Human-Wildlife Interaction

NHP Non-Human Primate

NNS Non-Native Species

No Number

I. INTRODUCTION

1. Human and Wildlife in the Anthropocene era

In 2011, scientists questioned humanity's impact on the Earth, wondering whether it was significant enough to define a new geological epoch (Jones, 2011). First introduced in 2000 by Nobel laureate Paul Crutzen, the term 'Anthropocene' is now widely accepted as marking the era in which human activities surpass natural geological and biological processes, profoundly shaping the planet's environment. While humans and wildlife coexisted and co-evolved for millennia (Marchini et al., 2019), two major revolutions—agriculture and industrialization—disrupted this balance (Lewis & Maslin, 2015), leading to ecosystem degradation and climate change, along with unprecedented declines in biodiversity (IPCC, 2019; IPBES, 2019). Nearly every terrestrial ecosystem has been impacted by human activities, with a staggering 94% showing signs of alteration (IPBES, 2019) and biodiversity loss is such that scientists now speak of a Sixth Mass Extinction (Cowie et al., 2022).

Habitat loss due to human activities is the first driver of decline in biodiversity (IPBES, 2019; Semenchuk et al., 2022). Intensive agricultural practices have degraded natural habitats more than any other human activity (Foley et al., 2005). By 2020, agricultural land accounted for 36.5% of the Earth's surface (World Bank, 2022). This relentless expansion is continuously reshaping the human-wildlife interface, as the shrinking of natural habitats brings humans and wildlife into closer proximity, altering the dynamics of their interactions in complex ways (Narayan & Rana, 2023). In these overlapping spaces, competition for land and resources has become increasingly imbalanced, resulting in heightened tension and a significant rise in negative interactions that often escalate into conflict and widely known in the scientific literature as Human-Wildlife Conflict (Anand & Radhakrishna, 2017; Conover, 2002; Messmer, 2009).

The introduction of non-native species (NNS) is the second greatest driver of human-caused extinctions worldwide, following habitat loss, and is responsible for approximately 40% of all species extinctions (Grosholz, 2005; Sax & Gaines, 2008). Ironically, these human-driven introductions create a unique form of human-wildlife interaction, where humans inadvertently generate conflicts with species, they themselves have brought into new environments. Introduced vertebrate species often adapt well to anthropogenic environments, where their presence can lead to significant economic damage, disease transmission, and increased

management costs (Jones et al., 2018; McNeely, 2001). Their resilience in human-modified landscapes not only heightens their impact but also increases the likelihood of conflict with local populations.

2. Human-Wildlife Conflict (HWC) or Human-Wildlife Interaction (HWI)?

Although the term "Human-Wildlife Conflict" (HWC) appears straightforward due to its explicit definition, the concept is more complex to grasp because of the multi-dimensional factors it involves and certain nuances that must be considered. In an attempt to capture the key elements that characterize such situation, IUCN SSC Human-Wildlife Conflict & Coexistence Specialist Group defines it as: “struggles that emerge when the presence or behavior of wildlife poses actual or perceived, direct and recurring threats to human interests or needs, leading to disagreements between groups of people and negative impacts on people and/or wildlife” (IUCN SSC HWCTF, 2020).

The term typically involves elements of interaction, intention, or recurrence. But most importantly, this definition also emphasizes the fact Human-Wildlife Conflict often goes beyond direct encounters between humans and wildlife and instead reflects underlying human social conflicts, such as economic disparities, cultural differences, and power imbalances within affected communities (Dickman, 2010; Madden & McQuinn, 2014). These social tensions can influence people’s responses to wildlife and drive conflict in ways that are not solely due to wildlife behavior.

However, beyond these social tensions, risk perception plays a crucial role in amplifying the sense of threat felt. Risk perception reflects an individual's subjective assessment of potential threats to their safety, property, or well-being (Smith, 2010), and it is often influenced by sociocultural factors (Dickman, 2010). This combination of social tensions and risk perception creates a complex framework in which human reactions to wildlife are heightened, even when damage control measures are in place (Kansky & Knight, 2014). For example, in Hindu communities, religious and cultural beliefs promote tolerance toward macaques due to their association with the monkey god Hanuman, a symbol of strength and devotion (Anand & Radhakrishna, 2017; Dore et al., 2017). This sanctity encourages the protection of macaques in sacred spaces such as temples; however, when these animals venture outside these areas to invade agricultural crops, risk perception increases, their sanctity erodes, and they become exposed to retaliation from farmers (Humble & Hill, 2016). Morphological factors, such as body

size, and demographic characteristics, such as large social groups or frequent crop feeding, can also contribute to an elevated risk perception of a species (Kansky & Knight, 2014). Riley (2007) found that while farmers reported macaques as the most frequent crop feeders, further investigation into cacao plantations showed that forest rats were responsible for consuming a much larger quantity of fruit than the Tonkean macaques (*M. tonkeana*)

This is also why choosing the right terminology is essential when discussing human-wildlife relationships. Framing these interactions solely as 'conflict' can misrepresent the risks posed by wild animals, exaggerating their threat to humans (Wilcove & Koh, 2010). Terms like 'crop raiding' and 'crop raiders,' which are often used in scientific literature to describe animals foraging on crops, may unintentionally suggest criminality or aggression on the part of wildlife. This language reinforces the idea that these 'conflicts' primarily concern wildlife harming humans. To foster a more balanced perspective, I will use terms such as 'human-wildlife interaction' (HWI) or 'Human-Wildlife Conflict and Coexistence' (HWCC) throughout this thesis. Similarly, expressions like 'crop-feeding' and 'feeders' are preferable, as they redirect the focus from controlling wildlife behavior to recognizing the deeper social, political, and economic dynamics at play among human stakeholders (Peterson et al., 2010)

3. Crop feeding as a major source of conflict between people and wildlife

Crop feeding has emerged as one of the most prevalent conflicts straining human-wildlife interactions (Hill, 2018; Nyhus, 2016). It refers to the behavior of wild animals leaving their natural habitats and encroaching on agricultural lands to consume or damage crops intended for human consumption. This activity can take two main forms: (1) animals actively feeding on standing crops, which diminishes yields meant for harvest, or (2) animals trampling or otherwise damaging the crops in their movement through the fields. Both forms result in significant agricultural loss (Naughton-Treves et al., 1998; Sillero & Switzer, 2001; Hill, 2017).

Crop damage by wildlife is a widespread issue across all inhabited continents and the precondition for it to occur is a spatial overlap. With farmlands currently covering approximately 38% of the global land surface and projected to increase by 70-100% by 2050 (Zabel et al., 2019), habitat loss and fragmentation are expected to intensify.

This shrinkage of wild habitats is generally most pronounced in developing countries with high biodiversity, such as tropical and subtropical zones, making numerous countries in Africa especially vulnerable to such conflicts (Bloomfield et al., 2020; Sillero & Switzer, 2001). In

these developing regions, where agriculture is a crucial part of the economy and livelihoods, such losses can greatly reduce the income of farmers. For instance, in Zimbabwe, a recent study reported that annual losses from wildlife damage to crops, property, and livestock ranged from US\$ 671 to US\$ 998 per household, representing 40–59% of the household's yearly income (Mhuriro-Mashapa et al., 2018).

In addition, beyond these tangible losses, the indirect effects of such conflicts—often harder to quantify—include opportunity costs. Increased stress levels and the need to invest more time and resources in protecting crops can detract from their ability to engage in other essential activities (Lee & Priston, 2005). In some cases, children may forgo school to assist in safeguarding crops, further impacting their education (Hill, 2017; Marchal & Hill, 2009). These indirect impacts, while less visible, play a critical role in exacerbating the challenges posed by human-wildlife interactions and can often lead to retaliatory actions against wildlife, posing serious threat to conservation efforts (IUCN, 2023). For example, the actual and perceived damage caused by the endemic Mauritian fruit bats (*Pteropus niger*) to commercial or substantial orchards has resulted in significant culls for five consecutive years from 2015 to 2018 and in 2020 (Kingston et al., 2023). These actions contributed to a decline in the species' conservation status from Vulnerable to Endangered (IUCN, 2018).

A range of wildlife species can damage crops with different levels of impacts depending on their geography. While certain species of insects, birds and rodents can cause severe loss worldwide - and sometimes even more than larger mammals - others are more geographically restricted and crop specific (Conover, 2002; Lahm, 1996; Naughton-Treves, 1997). White-tailed deer (*Odocoileus virginianus*) found in United States, wild boar (*Sus scrofa*) in Eastern Europe or elephant (*Loxodonta africana*) (*Elephas maximus*), found in Africa and Asia are often blamed for heavy damage to various types of crops (King et al., 2017; Manral et al., 2016).

Thus, crop feeding concerns various species and situations. However, this study will specifically focus on one of the most problematic crop feeders: non-human primates (hereafter, primates).

4. Human – Nonhuman Primate at agricultural interface

In just the past 30 years, agricultural land has expanded by more than 1.5 million km² into primate habitats, leading to increased proximity and frequent overlap in the use of space and shared environmental resources between humans and primates (McKinney et al., 2023; Waller, 2016). Since most primates are inherently tied to tropical forests, which are among the most threatened ecosystems due to agricultural expansion and deforestation, they are especially vulnerable to human activities (Estrada et al., 2017; FAO, 2023). As a result, like many other species, populations of non-human primates are declining with 93% of primate species in decline and 68% at risk of extinction (Estrada & Garber, 2022).

However, some primate species have adapted their behaviors in response to changes in their habitats (Fehlmann et al., 2020; McLennan et al., 2017), thriving in degraded areas near human activities, and include crops in their diets (Hill, 2000; Naughton-Treves et al., 1998). This adaptability has led many primate species to either forage in or establish permanent residences within agroecosystems (Estrada et al., 2017). As a result, crop feeding by primates has become a prevalent source of conflict, particularly in rural areas (Hill, 2005, 2018; Lee and Priston, 2005; Campbell-Smith, 2010). For instance, in Uganda, primates are responsible for over 70% of agricultural damage events and affect 50% of the damaged land area (Naughton-Treves, 1998).

Three cercopithecoid groups—vervet monkeys (*Chlorocebus* spp.), baboons (*Papio* spp.), and macaques (*Macaca* spp.)—are often labeled as agricultural "pests" (Hill, 2000, 2004, 2018; Naughton-Treves, 1997) defined as species whose negative impacts outweigh their benefits (Conover, 2002).

These species are highly adaptable due to their omnivorous diets and opportunistic feeding ecology, which can easily incorporate human-grown crops (Fehlmann et al., 2020; Hill, 2000; Saj et al., 2009). Their prehensile abilities allow them to grasp, dig, and carry food, and their semiterrestrial lifestyle enables them to exploit both ground and arboreal habitats (Adolph & Franchak, 2017). Their intelligence, curiosity, and complex social structures further enhance their capacity to adapt to human-dominated environments (Barrett et al., 2019). In addition, studies showed that primates can become more proficient at solving problems and innovating in response to human landscapes (Reader et al., 2011; Sebastián-Enesco et al., 2022). As a result, traditional protections such as barriers (e.g., electric fences, buffer crops) or behavioural deterrents (e.g., loud noises, bright lights, scarecrows, ultrasound) are often ineffective. It poses

an additional challenge for farmers to protect their crops leading to heightened negative perceptions and making conservation efforts to mitigate such conflicts even more difficult (Fuentes et al, 2011; Hill, 2017).

5. Factors influencing primates crop feeding behavior

Cultivated crops offer great benefits over wild food. They can provide high energy content, tend to be easier to digest than many wild plants and are spatially concentrated, reducing the search time for food (McLennan & Ganzhorn, 2017). Compared to the fluctuating availability of natural foods in human-disturbed habitats, crops also offer high predictability in both location and timing (Strum 2010; Reinegger et al., 2023). Therefore, it aims individuals to meet their nutritional needs with less effort (Strum, 1994; Naughton-Treves et al., 1998; Hill, 2017). Primates that forage on crops generally experience increased reproductive success, characterized by shorter interbirth intervals, as well as enhanced overall fitness (Strum, 2010). Overall, the frequency and intensity of crop foraging is influenced by many factors, briefly presented here.

a) ***Group size and demographic characteristics*** : Group size and individual characteristics (e.g., age and sex class) can influence crop foraging patterns (Strum, 2010; Wallace & Hill, 2012; Priston et al., 2011). For example, larger primate groups moved further onto farms and spent longer foraging on farms compared with smaller groups or solitary individuals (Hill, 2017). A bigger group can also lead to increased competition for wild food resources, prompting more frequent intrusion on agricultural lands (Hill & Lee, 1998).

The relatively few studies documenting age-sex class of primates foraging on crops have shown that adult and sub-adult males are primary offenders (Hill, 2017; Schweitzer et al., 2017; Strum, 2010). This may be attributed to their relatively high rates of exploratory behavior and risk-taking tendencies (Fuentes & Gamerl, 2005). Similarly, it has been shown that groups with a high proportion of juveniles are more likely to become agricultural pests (Quick, 1986), notably due to an inability to assess the level of risk (Saj et al., 2009). In contrast, adult females, especially those with infants feed on crops less frequently, likely due to their cautious approach, reflecting an increased awareness of the risks of foraging away from natural habitats (Fairbanks & McGuire, 1993).

b) ***Spatial patterns*** : Crop feeding patterns in primates are influenced by multiple interrelated characteristics of the landscapes they inhabit. While factors like the proximity of farmland to forest edges, rivers, and crop types have been well studied (Naughton-Treves, 1998; Hill, 2000; Saj et al., 2001), other spatial variables remain understudied, despite their potential significance. Species capable of behavioral flexibility in response to heavily modified habitats (Bloomfield et al., 2020), and able to exploit these changes, increase the risk of conflicts (Koirala et al., 2021), as seen in many primates that commonly feed on crops (Fuentes, 2011). Consequently, proximity to human infrastructures or roads can become important predictors of crop feeding behavior (Linkie et al., 2007; Riley, 2007).

Moreover, the reduction in forest cover, the fragmentation of natural habitats, and the expansion of agricultural land can collectively contribute to increased primate population densities, likely due to the enhanced carrying capacity offered by agricultural areas (Link et al., 2010; Torres-Romero et al., 2023). As forest cover diminishes, primates are increasingly forced to adapt their foraging behaviors, resulting in a greater reliance on agricultural crops (Wallace & Hill, 2012). This in turn leads to a rise in crop feeding incidents (Hill, 2000; Linkie et al., 2007).

c) ***Temporal patterns*** : Temporal factors, such as the time of day, significantly influence crop feeding patterns in primates. Research indicates that crop feeding often aligns with general circadian activity patterns, peaking during early morning and late afternoon while decreasing during midday (Hill, 2004; Koirala et al., 2021; Lamichhane et al., 2018). However, human activity can affect this pattern, as primates often change their foraging habits to avoid people (Bernstain, 1968; Gumert et al., 2011; Priston et al., 2012).

Seasonality also plays a crucial role in shaping crop feeding behavior since it determines both the availability of wild food in forests and the phenology of agricultural crops, including the presence of young leaves, flowers, and fruits at various ripening stages (Naughton-Treves et al., 1998; Strum, 2010).

During periods when wild food is scarce, crops can become a particularly attractive alternative for primates. Consequently, farmers who plant and grow crops during such lean periods in the forest may face increased crop foraging, as the scarcity of natural food drives animals to seek sustenance in cultivated fields (Lee & Priston, 2005). Many primates exhibit seasonal patterns in their crop foraging activities, increasing their reliance on crop foods during periods of reduced availability of wild foods. For instance, chimpanzees at Bossou, Guinea, and Bulindi,

Uganda, spend more time feeding on crops during periods of wild fruit scarcity (Hockings et al., 2009, McLennan, 2013). However, the positive correlation between crop feeding frequency and wild food scarcity is not always met (Hill, 2017). While certain crops are eaten in direct response to wild fruit scarcity, others are eaten according to their availability (Naughton-Treves et al., 1998; Seiler and Robin, 2016).

Yet, understanding spatio-temporal patterns determining the use of anthropogenic food by primates can improve effectiveness of mitigation measures (Hill, 2000; Linkie et al., 2007; Sitati et al., 2005; Sitati & Walpole, 2006). As a result, there is a need for context-specific research and adaptive management techniques to address crop feeding issues effectively.

6. Methods to monitor crop feeding by primates

a) **Camera trap** : To date, primate crop-feeding behavior has been studied using a variety of data collection methods, including indirect observations such as food remains, footprints, and species-specific feeding evidence like ripped stems and bite marks (Riley, 2007), fecal analysis (McLennan, 2013), as well as direct observations (Priston et al., 2012). While direct observation is advantageous because it enables researchers to collect detailed and precise information on individuals involved in crop feeding (Hockings et al., 2009), observing and quantifying primate foraging behavior in the wild poses several challenges, especially when primates are unhabituated to human presence, accustomed to being chased, and prone to flee upon contact. Additionally, human presence can alter primate behavior, and the habituation process of primates is time-consuming and raises ethical and health concerns (Palencia et al., 2022; Swann et al., 2011). Consequently, researchers have increasingly turned to new technologies as indirect methods such as remote sensor cameras or camera traps (CT), which offer advantages over direct observation (Krief et al., 2014; Piel et al., 2022). They collect data automatically, can be deployed in remote areas for extended periods, record on a 24-h cycle, and are noninvasive and minimally disruptive to wildlife (Caravaggi et al., 2020).

Camera traps can be an effective method for collecting additional data on various aspects of crop feeding behavior, including average group density, timing, duration and frequency of foraging bouts (Claridge et al., 2004) as well as the extent of damage caused (Caravaggi et al., 2020; Findlay, 2016; Zak & Riley, 2017).

Thus, camera traps can be a valuable tool for investigating crop feeding patterns in macaques. However, their effectiveness is further enhanced when combined with other methods. Complementary approaches, such as direct damage quantification (Riley, 2007) and engaging directly with farmers (Hill, 1997; Linkie et al., 2007), are essential to provide a more comprehensive understanding of post-crop feeding damage.

b) ***Quantifying crop feeding parameters and crop loss*** : Among the numerous negative impacts of crop loss on farmers' livelihoods, the loss of income due to damaged crops represents one of the most significant issues (Ango et al., 2017; Sillero & Switzer, 2001). One of the most effective ways to evaluate the success of a crop protection method is by measuring crop loss relative to the costs incurred and the effort exerted by farmers (Wallace & Hill, 2012; Wallace, 2010). Furthermore, methods that directly mitigate damage not only have the most substantial positive effect on crop yields but also deliver considerable value to farmers (Conover, 2002). Therefore, accurately assessing crop losses is essential for the effective implementation of these protective strategies. However, quantifying crop damage systematically is difficult and time-consuming. Several methods have been used to assess damage, such as enclosure plots (Priston, 2009), vegetation quadrats (Naughton-Treves et al., 1998), line transects (Priston & Underdown, 2009), and farmer estimates (Linkie et al., 2007). Yet, no single method currently garners consensus in the literature, which complicates comparisons between studies (Plumptre et al., 2013). Despite these challenges, specific attributes of crop feeding events (CFEs) — such as feeding frequency, duration of CFEs, and average group size of feeders — can be key parameters for quantifying crop loss as they directly affect the extent and severity of damage (Findlay & Hill, 2020; Wallace & Hill, 2012). For instance, Findlay (2016) demonstrated that these factors are positively correlated with increased crop damage. Furthermore, identifying and quantifying these parameters prior to implementing mitigation strategies is crucial, as it allows for a better understanding of which behavioral aspects should be targeted by deterrents to reduce crop feeding and manage conflict.

Yet, few studies rigorously quantify these parameters or establish clear connections to the amount of damage incurred during a CFE (Findlay, 2016; Wallace & Hill, 2012).

c) ***Ethnoprimateology*** : Documenting crop losses faced by individual farmers or communities does not necessarily capture the full impact of primate interactions on their

livelihoods. For example, the extent of damage at the community level often falls within the thresholds deemed acceptable in large-scale mechanized farming systems (10-15%). Nevertheless, farmers tend to regard wildlife-induced crop losses as a significant issue (Hill, 2018; Hill, 2004). Moreover, negative perceptions of certain species can exacerbate the sense of conflict, even when steps have been taken to mitigate the damage (Kansky & Knight, 2014). Thus, it is crucial that any efforts to reduce human-nonhuman negative interactions take into account the region's socio-ecological and economic context, rather than merely addressing the immediate causes of the conflict. This broader approach ensures long-term solutions that align with the complex interplay of environmental and social factors in the area (Wallace & Hill, 2012). Ethnoprimateology is a relatively new discipline, examining the long-standing interactions between humans and primates, exploring both ecological and cultural relationships. This approach studies how humans and primates share resources and spaces (Hockings et al., 2009; Riley, 2006) while also analyzing cultural connections and beliefs. It draws on anthropological tools like critical analysis to better understand these complex dynamics (Fuentes, 2011; Malone et al., 2014).

The ethnographic approach reveals attitudes that are highly complex, context dependent, and constantly changing. Combining quantitative data with qualitative methods allows for a more complete understanding of human-primate interactions (Linkie et al., 2007; Setchell et al., 2017).

7. The Long-Tailed Macaque in Mauritius: a generalist and synanthropic introduced species

Order: Primates

Suborder: Haplorrhini

Infraorder : Catarrhini

Family : Cercopithecidae

Sub-family : Cercopithecinae

Genus : *Macaca*

Long-tailed macaques (hereafter LTM) or crab-eating macaques or cynomolgus monkeys (*Macaca fascicularis* Raffles, 1821) is a catarrhine primate belonging to the subfamily Cercopithecinae (family Cercopithecidae) (Napier and Napier, 1967).

Considered as the third most widely distributed primate species after humans and the rhesus macaque (*M. mulatta*), the long-tailed macaque has a distribution that ranges from Myanmar

to the island of Timor, extending north to south, and from the Philippines to Bangladesh, spanning east to west (Fooden, 1995; Ruppert et al., 2022). There are also cases of ethnophoresy where long-tailed macaques have been introduced to some oceanic islands beyond their original range. Such cases are reported in West Papua, Hong Kong, Palau and Mauritius where it was introduced around the seventeenth century (Sussman and Tattersall, 1986). The context of introduction to Mauritius would be discussed a bit later.

In their native range, they can be found in various habitat types including primary or secondary forests, riverine and coastal forest, mangrove and nipa swamp, as well as secondary forest (Fuentes, 2011). Due to their high ecological and cognitive flexibility, they frequently exploit areas influenced by human settlement and agriculture often adjacent to forest (Gumert et al., 2011). This increasing tendency to inhabit areas at the edges of human-dominated spaces has led to their classification as an « *edge* » species (Fuentes, 2011).

The social organization of the long-tailed macaque is characterized by multi-male, multi-female groups where females are philopatric and matrilineal, forming strong lifelong bonds with their female relatives. The sex ratio is variable but generally skewed toward females due to their extreme philopatry: females remain in their natal group for life, forming a stable social core of related females (Wrangham, 1980). In contrast, males migrate regularly throughout their lives, approximately every 4-5 years (Van Noordwijk & Van Schaik, 1987). The group size of long-tailed macaques typically ranges from 15 to 50 individuals. However, it can vary significantly depending on habitat disturbance, with larger groups found in more human-altered and provisioned environments (Brotcorne, 2014). Their lifespan can reach up to 25 years, with a high reproductive rate (one offspring per year in average), as females are capable of breeding year-round (Ross, 1992; Thierry, 2007).

Macaques are primarily frugivorous, but their diet also includes leaves, seeds, mushrooms, and small invertebrates like insects and crustaceans (Fooden, 1995). Their adaptability to human environments allows them to exploit human food sources (Fuentes, 2011). The expansion of land transformation due to human activities, particularly large-scale agriculture, creates many transitional zones between human and forest habitats. As a result, macaque groups shift away from forests, emphasizing their opportunistic ecology. They increasingly focus on agricultural areas bordering forests as a source of food, or even on urban habitats, which lead to increasing frequency of interaction with humans (Fuentes, 2011; Gamalo et al., 2024).

8. Success of colonization in Mauritius

Cases of ethnophoresy are various since long-tailed macaques have been introduced out of their native range onto at least four islands: Palau (Poirier & Smith, 1974), West Papua (Kemp and Burnett, 2003), Sulawesi (Froehlich et al., 2003), Tinjil Island near Java (Kyes, 1993) and Mauritius (Sussman & Tattersall, 1986). However, only two islands reported important impacts: Mauritius and Palau. The success of the colonization on these islands can be explained by two main factors:

a) ***High levels of habitat destruction:*** In Mauritius the local fauna is highly sensitive to human induced alterations (Cheke & Hume, 2008; Cheke, 1987; Hammond et al., 2015). As a result, many native species, like the dodo, emblematic of this loss, became extinct within a century of human colonization. In parallel, long tailed macaques have been documented to cope with severe environmental damage (Berenstain, 1986). This may give long-tailed macaques an advantage in stochastic environments compared to local fauna.

Since its initial colonization in 1638, Mauritius has experienced massive habitat destruction. Today, almost 60% of the island's area has been modified by humans and only 4.4% of native forest remains (Hammond et al., 2015).

In addition to becoming a popular tourist destination, Mauritius is the most densely populated country in Africa, with nearly 1.3 million inhabitants spread over an area of 1,865 km² (Statistics Mauritius, 2023). The urban development required to accommodate this growth, combined with ongoing agricultural activities, significantly reduces the available space for natural habitats.

b) ***Easily accessible crops and human resources:*** In Mauritius, about 55% of the island's total land area is devoted to agricultural use, with sugarcane remaining the dominant crop (Nigel et al., 2015) and 5.5% is occupied by built-up areas. These expansive agricultural landscapes —often exceeding hundreds of hectares—provide easy access to stable food resources with little or no competition from the local fauna. Human agriculture and food sources play a crucial role in supporting macaque colonization.

This hypothesis is supported by the fact that in other islands such as in Papua or Kabaena where long-tailed macaque has been introduced no major expansion of macaque's populations was reported, remaining stable since decades (Froehlich et al., 2003). Both have lower levels of anthropogenic habitat alteration and limited crop base in their farmlands (Diamond, 1997).

Thus, the combination of habitat disturbance and anthropogenic food sources may have facilitated establishment of macaques outside of their native range. It appears that human impact is the key for allowing successful macaque colonization on an island.

9. Human-macaque interface in Mauritius

The long-tailed macaque (*Macaca fascicularis* Raffles, 1821) was introduced in Mauritius ~400 years ago by either Portuguese or Dutch (Cheke & Hume, 2008). It is not clear whether they were released deliberately or accidentally, but recent genetic work suggests there were very few original founders (Kondo et al., 1993). In the absence of predators, the population has thrived and grown in tandem with the human population over time. Today, they are found almost throughout the island, inhabiting a variety of habitats each supporting different densities of macaques. Although detailed data on the wild population are lacking, estimates from the 1980s placed the number between 30,000 and 40,000 individuals.

The human-macaque interface in Mauritius while complex, remains poorly studied (Sussman et al., 2011). Part of the population reveres the monkeys due to religious beliefs, particularly within the Hindu community, where some consider them sacred. However, in the more natural habitats, macaques are labelled as an invasive alien species (IAS), with concerns about their role in spreading invasive plant seeds such as Chinese Guava (*Psidium cattleianum*) (Florens, 2013), competing with native species like the Mauritian flying fox (*Pteroptus niger*) (Reinegger et al., 2021, 2023) and negatively impacting threatened species such the endangered Pink Pigeon (*Columba mayeri*) (Cheke, 1987).

Furthermore, macaques are recognized as a significant agricultural threat, with their impact on farming practices—particularly regarding sugarcane and vegetables—well-documented over several decades, if not centuries (Lyons & Miller, 1999). However, there seems to be a lack of thorough assessment of the full extent of this impact

According to Carié (1916), as early as 1712, the Dutch decision to abandon Mauritius was partly due to the significant damage rats and monkeys inflicted on their plantations. Since then, commercial farmers have continued to report notable crop losses due to long-tailed macaques, with estimated damages reaching up to £1-2 million annually (Bertram, 1994). These macaques target both sugar cane and vegetable crops. Sugar cane, which requires an 18-month maturation period, is especially vulnerable because macaques cause damage at every stage of growth (Hill, 2000). In addition, the year-round cultivation of various vegetables attracts macaques, who

tend to inflict more damage than they consume. Reports show that agricultural damage peaks during July and November, coinciding with the end of the dry season when wild food resources are scarce (Bertram, 1994; Sussman & Tattersall, 1986).

Due to their perceived overabundance and reputation as "destructive pests", combined with local pressures for population control, macaques in Mauritius have increasingly become targets for biomedical research (Bertram, 1994). For over a decade, Mauritius has ranked among the world's top exporters of *M. fascicularis*, with the trade significantly bolstering the economy; a single macaque can fetch up to \$24,000, making it the second-highest-value animal in global trade (Chowdhury, 2024; Hansen et al., 2022). Breeding facilities have proliferated across the island to house macaques captured directly from the wild. It is estimated that the number of macaques in captivity rivals that of those in the wild, with approximately 40,000 individuals held in captivity (Sussman et al., 2011).

Because the capture for biomedical purposes raises ethical concerns and is generally unpopular with the public, there is a growing need for alternative, non-lethal mitigation strategies (i.e., sterilization campaigns, effective deterrents). However, these strategies often require a deep understanding of primates' foraging behavior to ensure their effectiveness (Hill, 2017). Despite this, the long-tailed macaque's prominence in medical and laboratory research has led to a disproportionate number of studies focused on its physiological and experimental aspects, rather than its behavioral and ecological characteristics (Naughton-Treves et al., 1998; Seiler & Robbins, 2020).

To the best of our knowledge, no study has yet explored the crop feeding behaviors of long-tailed macaques in Mauritius. This represents a significant gap, given the species' pervasive presence in the cultural and ecological landscape of the country and the growing challenges it poses to local agriculture and human-wildlife coexistence.

10. Study objectives

This research project aims to characterize interactions between macaques and farmers in the context of crop foraging in Mauritius. Specifically, it investigates ecological and biological factors that influence macaque crop foraging patterns, using camera traps, crop damage measurements, and phenological data. Questionnaires are also applied to assess farmers' perceptions of macaques, exploring their attitudes and nuisances they experience. The research focuses on three primary objectives:

- 1) Analyzing the effects of spatial factors (e.g., landscape physical features), temporal factors (e.g., fruit availability), and demographic characteristics (e.g., group size and age category) on macaques' crop feeding activity (e.g., duration, weekly crop feeding frequency).
- 2) Identifying which crop feeding parameters — fortnightly crop feeding frequency, duration and the number of individuals involved — best represents crop damage in each field, using the count of crop items removed by primates as a proxy for estimated damage.
- 3) Investigating farmers' perceptions of macaques in areas highly impacted by crop foraging through structured questionnaires to assess their attitudes, and nuisances they faced.

11. Hypotheses and predictions

1. Assessment of the effects of spatial, temporal and demographic parameters on macaque crop feeding activity.

- (a) As macaques likely face more deterrents when humans are present in crop field, we predict an increase in crop foraging intensity during the early morning and late afternoon when human activity drops.
- (b) As seasonality seems to be the most important factor in predicting crop feeding behavior (McLennan & Ganzhorn, 2017; Naughton-Treves et al., 1998), we predict that crop foraging frequency and duration will increase when fruit availability is scarce.
- (c) As the availability of fruit declines with decreasing forest cover, we predict that macaques will increasingly rely on crops in areas with less forest cover. Therefore, the extent of surrounding forest cover is expected to have a negative correlation with both the frequency and duration of crop foraging by macaques.
- (d) As it generally requires more effort and resources to protect agricultural areas that are increasingly remote and isolated, we predict that the greater the distance human infrastructure, the higher the frequency and duration of crop feeding by macaques

2. *Estimation of crop feeding parameters - frequency, duration and number of individuals involved - as best indicator for crop damage in each sugarcane field, using the count of crop items removed by primates as a proxy for estimated damage*

- (e) We hypothesize that the frequency per fortnight, duration, and number of individuals involved in crop feeding will be positively correlated with the damage recorded, with the number of individuals being the strongest predictor of damage.

3. *Investigating farmers' perceptions of macaques in areas highly impacted by crop foraging*

Socio-cultural variables such as religion, age, profession, and educational background are crucial in shaping human social identity (Dickman et al., 2010). These variables influence personal beliefs, which form the foundation of individual values. Based on this, we predict that:

- (f) Due to the cultural significance of monkeys in Hinduism, Hindu farmers are expected to show greater tolerance towards macaques compared to other religions.
- (g) Younger people having more exposure to education are anticipated to be more tolerant towards macaques than older people.

II. MATERIAL AND METHODS

1. Study area

This study was conducted in Mauritius, located in the Indian Ocean (20°17'S, 57°33'E). The island's volcanic origin has given rise to significant local variations in topography, as well as a notable climatic diversity, despite its relatively small size of only 62 km long and 45 km wide. Mauritius is characterized by two major geographical zones: the upland and lowland regions, which exhibit distinct climatic and vegetative differences. The upland zone, typically above 500 meters, experiences cooler temperatures and higher rainfall, with tropical montane forests that support significant biodiversity and many endemic species. Annual rainfall can exceed 5,000 mm, creating a lush, humid environment. In contrast, the lowland areas, near sea level, have a warmer climate and receive less rainfall, especially along the coast. The tropical climate is composed of a warm, wet summer occurring from November to April followed by a cool, dryer winter from May to October, with a mean annual air temperature of 22°C (Padya, 1989)

Sugarcane dominates agriculture (98% of cultivation and 55% of the island surface area), yet represents less than 3% GDP. Other agriculture includes fruit, tea and vegetables. Scrub, forests and plantations cover 38% and approximately 6% of the land is under urbanization (Hammond et al., 2015; Nigel et al., 2015). The majority of the population practices Hinduism (48%), followed Christianity (32%) and Islam (18%), reflecting the island's religious diversity (Central Statistics Office, 2022).

The research was conducted from June to September 2024 at forest-agriculture interfaces across six different sites on the island (Figure 1). This period coincides with the dry season, which is known to be when macaque-related damage is most frequent (Bertram, 1994). Four of the sites were located within large sugarcane plantations (Alteo and Medine), two of which were each characterized by distinct forest types and climates. Medine has semi-arid vegetation, with rainfall often below 1,000 mm per year, while Alteo, situated in one of the island's rainiest areas, supports lush, wet forest vegetation, with annual rainfall reaching up to 3,600 mm. The other two sites were smaller plantations dedicated to vegetable cultivation. The first was a mixed garden cultivated with eggplant (*Solanum melongena*) located in a subhumid region with an annual rainfall of around 2,000 mm. The second, Plaine Sophie, is dedicated to the cultivation of chayote (*Sechium edule*, locally known as “Chouchou”), which thrives in cooler

and much wetter conditions (Biquand & Biquand-Guyot, 1992; Struhsaker & Siex, 1998). Detailed information about each site is provided in Table 1. All sites were relatively isolated from human infrastructure and bordered by forests, whose type, degree of degradation, and fragmentation varied. These sites were selected for (a) their vulnerability to crop-feeding by macaques, (b) their representation of the island's diverse crop types and agricultural practices, and (c) the support of local farmers for the research objectives. Breeding facilities occasionally conduct trapping around the sampled sites.

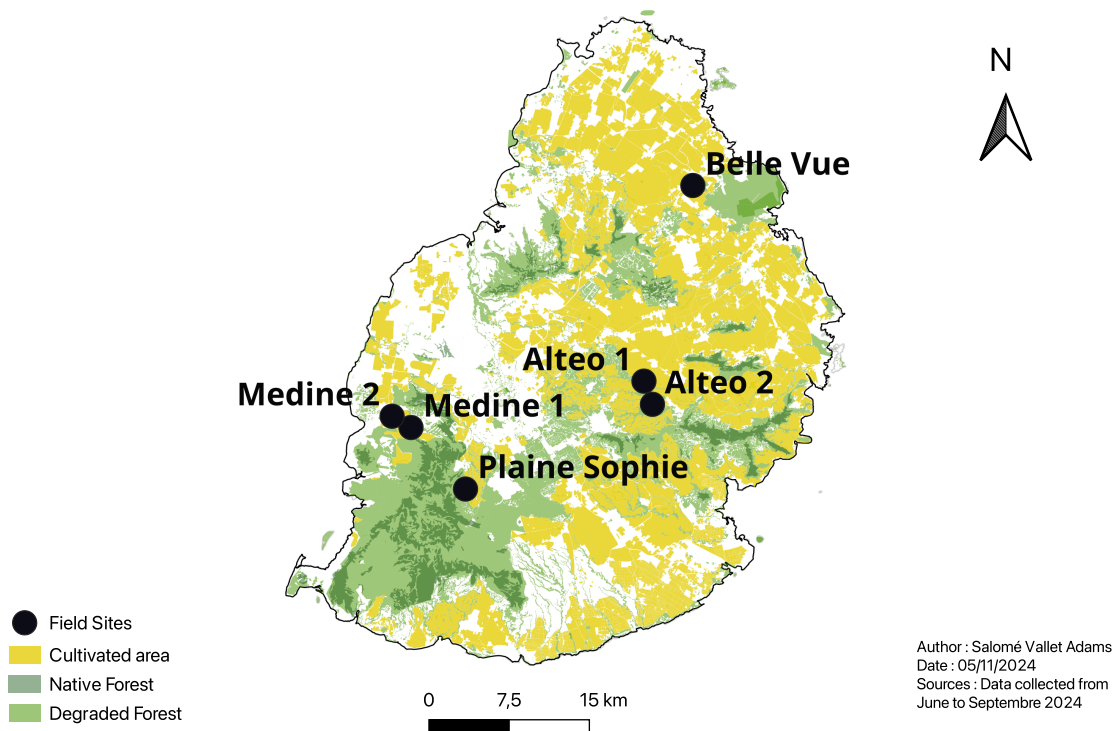


Figure 1. Map showing the field sites where camera traps were set-up between June 2023 and September 2024 and land use in Mauritius.

2. Data collection on crop feeding parameters

2.1. Camera trap

Browning Ops Elite 22 Camera Traps were used to survey each of the six crop fields (N = 6 camera traps) from June to September 2024. They were positioned along each crop-bushveld edge, at appropriate angles at approximately 0.7 m above the ground. All the cameras faced onto the farms and were secured using multiple lengths of coated flexible wire and a padlock to prevent theft (Appendix 9). The following information was collected after setting up the camera trap: camera ID, type of crop, GPS coordinates, date and number of trap-days. Total sampling effort for this study covered a total of 507 camera-days; details are shown in Table 1.

Table 1. Details of camera trap (CTs) sites, including crop type, location (Latitude, longitude), and number of camera- days for each site.

Sites	Type of crop	Size of the field (m ²)	CTs location	No ¹ . of camera-days
Alteo 1	Sugar cane	30766.02	(-20.2872199, 57.6295352)	106
Alteo 2	Sugar cane	12591.44	(-20.3069899, 57.6389524)	106
Medine 1	Sugar cane	41420.67	(-20.3166931, 57.4037056)	45
Medine 2	Sugar cane	111116.19	(-20.3271789, 57.4187907)	97
Bellevue	Eggplant	1519.1	(-20.1229532, 57.6735117)	81
Plaine Sophie	Chayotte	6502. 41	(-20.3777627, 57.4693024)	72

¹“No.” refers to “Number”

The cameras were set up to record high-definition videos of 20 seconds (up to 18 m), with a 20-second interval between triggers. For each video the following information was automatically recorded: date, time, temperature. Cameras were operational 24 h a day and batteries were changed when the camera's battery life indicator showed 50% remaining. We used a 32 GB memory card which was replaced with a blank one every two weeks. All video footage was analyzed with the software Timelapse (Version 2.3.24) by a single observer.

We employed a targeted opportunistic sampling method in specific, non-systematic areas to observe crop-feeding behavior of macaques (Caravaggi et al., 2020b; Fegraus et al., 2011). Camera trap locations were selected following an initial visit to the field with the landowners and were set up based on farmers' willingness to participate, their knowledge of macaque access points, and practical considerations such as wind and vegetation. Given the exploratory nature of this study and the limited resources available, we prioritized efficiency and strategic placement of cameras. For the two vegetable gardens (Bellevue, Plaine Sophie) due to their small size (range: min = 1819 m²; max = 6502 m²), one camera was sufficient to record all visits by macaques. In sugarcane fields (Alteo 1, 2, Medine 1, 2), despite their large size (min = 1519 m²; max = 111116 m²), cameras were placed at locations where macaques appeared to regularly enter and exit the fields. At the start of the study, we surveyed the entire field for these feeding signs by visual observation, which helped identify key locations frequently visited by macaques. We confirmed that macaques used limited entry points by comparing damaged sugar cane stems between plots near entry points to plots without feedings signs every two weeks (Appendix 8a and 8b). These behavioral patterns suggest that macaques prefer certain access points where access to sugarcanes is easier, resulting in regular and predictable entry routes.

While preliminary field observations were conducted to familiarize with the study sites and macaque behavior, all data used for analysis were collected exclusively from camera trap recordings. We defined a crop feeding event (CFE) as any instance in which one or more macaques were detected by the camera. We considered a CFE independent if more than 30 minutes had passed since the previous video of the same species. This time interval was selected based on the mean recorded durations of CFEs from preliminary camera trap data. For each CFE, we recorded their duration and frequency for each site. We also recorded the number of individuals and their age/sex categories actively feeding on crops. Given the challenge to identify all age-sex classes from the videos, we limited to the classification of individuals into two distinct age categories that could be clearly distinguished in the camera trap footage: adults and juveniles. To estimate the number of individuals for each CFE, we recorded the maximum number of macaques observed at a given time on the videos of a single crop feeding event.

3. Collecting data on spatio-temporal factors influencing crop foraging patterns

3.1. Spatial parameters

To investigate which spatial predictors influenced the likelihood of crop feeding by macaques, key variables were extracted for each study area including anthropogenic and natural variables. Distance to the human settlements, percentage of farmland and percentage of forest cover were measured. The extraction of these variables was performed manually using QGIS software based on satellite imagery (Google Satellite) and open-access data available online. The spatial scale ('buffer') used to calculate each variable was 1 km², corresponding to the average home range of a long-tailed macaque group (Sussman et al., 2011; Berenstain, 1986).

3.2. Phenological data

To assess wild fruit availability in the forests surrounding the crops, three transects were randomly established per study site within the theoretical macaques' home range (A total of 12 transects). Each transect was 5 meters wide and 200 meters long. All trees with a DBH (diameter at breast height) ≥ 5 cm were tagged and identified, and all vines present on the trees were recorded (Chapman et al., 1992, 1994). The phenological state of each tree was determined monthly on predetermined dates by visually examining them with binoculars to note the presence or absence of young leaves, ripe or unripe fruits, and flowers. Food availability indices were calculated as the ratio of the number of tagged trees or vines bearing fruits, flowers, or young leaves to the total number of trees monitored in each study site. For

trees with unknown species, a sample of leaves (and sometimes fruit) was collected, dried, and sent to The Mauritius Herbarium for species identification.

Despite the small sampled area (0.3 ha per site), the sampling effort provided an adequate representation of the vegetation. Each transect allowed the collection of phenological data for at least 15 trees per plant species per site, which is the minimum number recommended for estimating plant phenology in tropical forests (Morellato et al., 2009), except for forests with rare species. However, the forest communities at each site were all highly degraded and homogeneous, mainly including *Ravenala* forest and savannah and thorn scrub (Vaughan & Wiehe, 1937).

Phenology data were analyzed by creating a fruit availability index, which was calculated by taking the mean abundance scores for each species per month and dividing the sum of the composite scores by the number of species in the sample. Indices were calculated for fleshy fruits only, and for ripe and unripe fruits combined (McLennan, 2013; Riley, 2007). All species and index fruit for each site can be found in Appendix 6.

4. Quantifying macaque damage to sugarcanes

4.1. Defining and quantifying macaque ‘damage

To assess the extent of macaque damage, we employed a transect-based method, recording the number of crop items removed by macaques every two weeks. A 20-meter-wide transect was placed parallel to the field edge (transect width parallel to field width), starting at the camera trap location and aligned with the camera's field of view.

The field edge was defined as the first row of sugarcane plants containing at least five plants over a 20-meter stretch along the field width, as plants in this initial row were often heavily damaged or absent (Appendix 8c). To determine the length of the 20-meter-wide transect, we initially selected four random points along the transect (Fig. 2). From each selected point, we assessed the damage caused by macaques to sugarcane plants along a 1-meter-wide line transect, spanning the length of the field and running perpendicular to both the field's width and the forest edge (Fig. 2). The maximum depth of damage recorded across the four perpendicular transects was used to determine the final length of the 20-meter-wide transect. The maximum depth of damage recorded across the four perpendicular transects was used to determine the final length of the 20-meter transect. Consequently, it covered the area where most of the macaque damage occurred from the field edge.

We then sampled macaque damage every 15 days for each sugarcane site by counting all damaged stalks along the 20-meter transect, line by line. To distinguish between 2-week-old and 3-week-old (or older) damage to sugarcane stems, we simulated macaque damage by breaking and pulling three sugarcane stems adjacent to each study site. We marked these stems and photographed them weekly to track the progression of damage (Fig. 3).

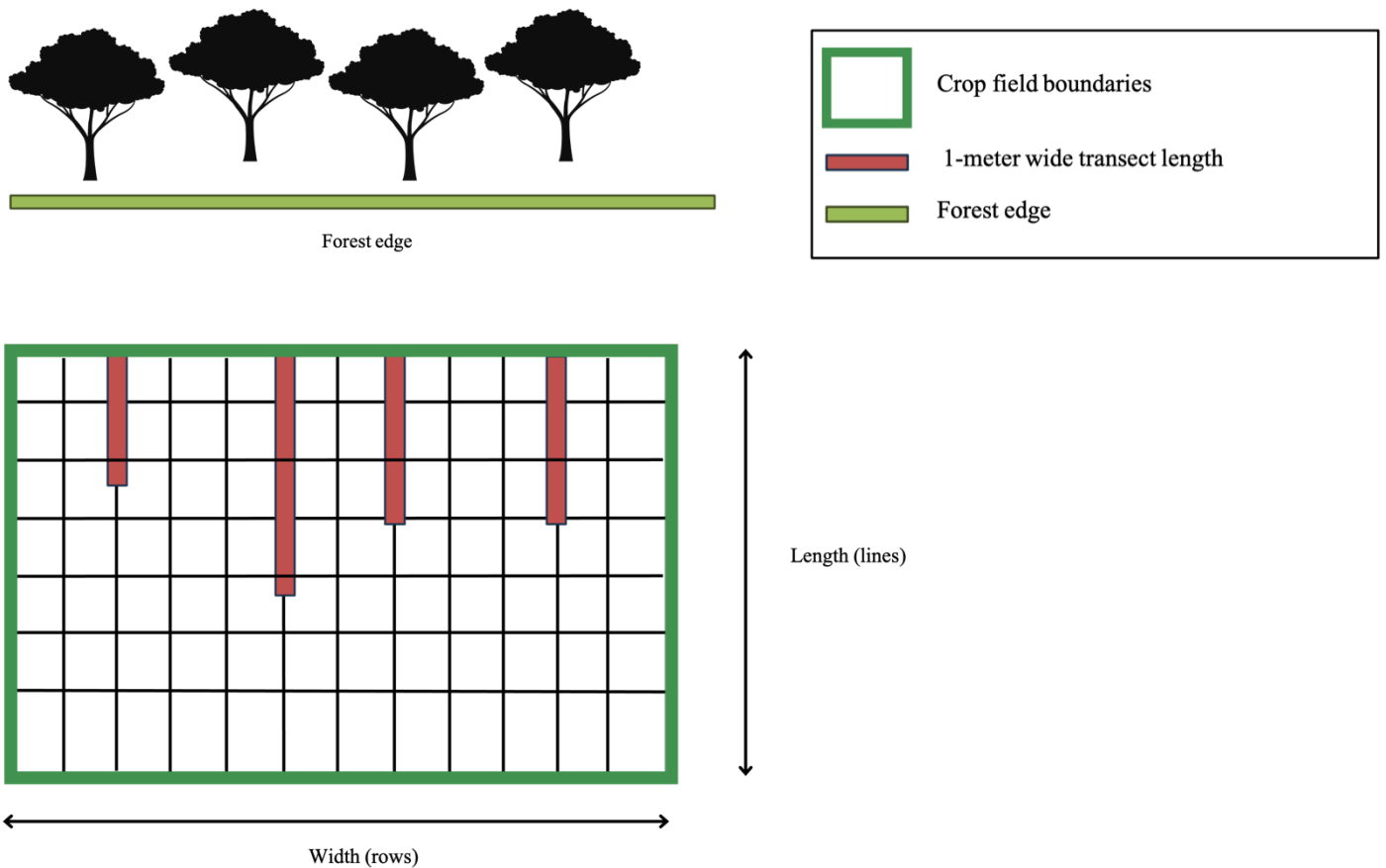


Figure 2. Method for assessing the extent of macaque damage in sugarcane fields using four perpendicular transects, where the maximum depth of damage determined the length of the final 20-meter-wide transect where damages were recorded every 15 days.

We were able to distinguish damage caused by macaques, wild boars, and rodents, based on their distinct feeding behaviors on the cane (Fig. 4). Detailed observations of damage for each field are provided in Appendix 10.



Figure 3. Evolution of a sugar cane stalk after breaking (a) few minutes old (b) 2 weeks old (c) three weeks old.



Figure 4. (a) Sugar canes broken by macaques. Usually, they break or pull it. (b) Rodents damage both roots and portion of the stalk internode usually near the base of the cane, leaving part of the outer stem intact (c) Wild pigs damages are clumped in the center of the field and can be recognized by trampled stalks lying on the ground.

Finally, to demonstrate that the observed damage patterns were specifically associated with macaque activity and not occurring universally across all fields, we selected a control field and placed a transect of similar dimensions in order to have a baseline for comparison. We identified one control field for each sugarcane site (N = 4) which remained the same for the entire duration of the study. It was chosen by walking along and within each field, selecting an area that showed no evidence of monkey damage (i.e., No dragged canes, old leaves or broken canes) (Appendix 8a, 8b.). If the entire field edge was damaged, we chose the nearest field with no direct evidence of monkey damage.

In vegetable fields, damage quantification could not be conducted. In the case of chayote (commonly called "Chouchou" in Mauritius), macaques were removing the vegetables from the fields and transporting them directly into the forest, making damage estimation impossible. For eggplant, the methodology used for assessing vegetable damage was not applicable to sugarcane fields, leading to non-comparable results.

5. Socio-cultural data collection

A questionnaire survey was conducted to assess human perceptions and attitudes toward macaques, as well as the nuisances caused by them. The participants included farmers from areas affected by macaque crop feeding across the island. A total of 55 individuals were interviewed between July and September 2024. Efforts were made to ensure that local residents had an accurate understanding of the project and realistic expectations regarding potential outcomes. Initially, some participants mistakenly believed the project was linked to a breeding facility and that assistance could be provided to trap monkeys near their plantations. Care was taken to clarify the purpose of the study. During the interviews, a neutral stance was carefully maintained regarding the issue of crop feeding to minimize any potential influence on participants' responses. The questionnaire (Appendix 1) was conducted orally, either in French or Creole, with the assistance of a local interpreter for Creole when necessary. On average, each interview lasted 15 minutes. Participants were informed in advance about the anonymous nature of the interview and their right to withdraw at any time (Appendix 1). Before starting each interview, preliminary information was recorded, including the date, start time, location, and GPS coordinates.

The questionnaire consisted of 45 questions divided into four main sections. The first section gathered socio-cultural data, including gender, age, profession, education level, and religion.

These variables were chosen to analyze socio-cultural predictors influencing perceptions and attitudes toward macaques. The second section focused on respondents' attitudes toward macaques in general. This attitudinal information (Manfredo, 2008) explored participants' perceptions and emotions regarding macaques (e.g., feelings of fear, perceptions of macaque aggressiveness, beliefs about the sacredness of macaques) as well as self-reported behaviors (e.g., willingness to tolerate macaques taking a small portion of the crops, hunting them). The final section gathered detailed information on macaque crop feeding behavior (e.g., frequency of visits and the number of individuals involved). It also explored the methods used to deter macaques, the presence of traps around plantations, and participants' opinions on trapping, including whether they supported or opposed its use and their perceptions of its effectiveness.

Table 2. Sample of respondents with the numbers for each socio-cultural variable. “Secondary Sup” referring to “Secondary Superior”. Muslim and Christian were combined into one category “Other religions”.

Gender	Age		Education		Religion		Planteur full time		
♂	50	< 30	12	No Education	5	Hindu	37	Full-time	46
♀	5	30-51	19	Primary	7	Muslim	15	Part-time	9
		> 51	20	Secondary	25	Christian	3		
				Secondary Sup	13				
Total 55									

6. Statistical Analyses

All statistical analyses were performed using RStudio software (v. 4.4.2) (Rore Team, 2024). All tests were conducted with a significance threshold set at 0.05.

6.1. Crop feeding event parameters and temporal distribution of feeding events

Descriptive statistics were used to analyze CFE parameters (i.e., duration, frequency, and number of individuals) as well as CFEs temporal distribution. Kruskal-Wallis test was used to compare CFEs duration across sites and Chi-square tests were conducted to examine the variation in CFEs frequency across four time periods: 6 am-9 am, 9 am-12 pm, 12 pm-3 pm, and 3 pm-6 pm.

Subsequently, we aimed to determine whether the temporal patterns of macaques aligned with (or diverged from) those of humans in sugarcane and vegetable fields, respectively. Since videos featuring humans could not be classified as distinct event as we did for macaques, we used the number of occurrences (all videos) of both macaques and humans across all sites. We

then compared the frequency of occurrence of the two species (macaques vs. humans) for two time periods for sugarcane and vegetable fields: morning (6:00 am –12:00 pm) and afternoon (12 pm–6 pm) by conducting a Chi-squared.

6.2. Most influential predictors explaining CFE duration and frequency

6.2.1. CFEs duration

To determine which predictors were likely to influence the duration of CFEs, we used a Generalized Linear Model (GLM). The response variable was the duration of CFEs (in minutes), with fixed explanatory variables including the number of individuals, the proportion of adults in the group, the distance to the nearest buildings, the proportion of farmland or forest within a 1 km radius, the Fruit availability index, and the site. Given the small number of sites ($N = 6$) and the limited number of experimental units (one replication per site), we followed Oberpriller et al (2022) and treated '*Site*' as a fixed effect (instead of random effect) to avoid bias and imprecise estimates that could arise from random-effect modeling in such cases (Harrison et al., 2018). We first conducted an exploratory analysis to generate hypotheses about predictors of CFE duration (Bissonette, 1999), following methods outlined by Tredennick et al (2021) to balance testing many plausible covariates while minimizing false discoveries. CFE duration was then plotted against each of these six explanatory variables, and Spearman's correlation coefficients was calculated to assess the strength and nature of the relationships. Only predictors with Spearman's correlation coefficients ≥ 0.1 (excluding Fruit availability index and distance to buildings) were included in the final GLM.

We then fitted a global model with the selected predictors using a Generalized Linear Model. We fit the GLM with lognormal error distribution (using package *glmmTMB* – Magnusson et al. 2021), to obtain a normal distribution of the response variable (CFEs duration). We calculated variance inflation factor (VIF) values to confirm collinearity between predictors was not an issue (VIF values < 3) with the function *corvif()*.

We then evaluated model fit of the global models using residual diagnostic plots from package DHARMA (Hartig 2022). As a final step, we fit a series of reduced models in which one of the predictors was dropped in each model, and compared them to the global model using likelihood ratio-tests, correcting P-values for multiple comparisons using the Benjamini and Hochberg method (Benjamini & Hochberg, 1995). We reported the model estimates together with their standard errors (SEs) and 95% confidence intervals (CIs) to evaluate their accuracy and reliability (Nakagawa & Cuthill, 2007) and made general conclusions about their direction (Bissonette 1999).

6.2.2. *Weekly frequency of CFEs*

To assess the factors influencing the frequency of CFEs, we used the number of CFEs per week. We then applied Generalized Linear Model (GLM) to analyze the data. The response variable was the weekly count of CFEs, while the predictors were the same as those previously mentioned, with the exception of the total number of individuals, which was excluded due to its near-perfect correlation with the response variable, as it increases linearly with each additional event.

Our preliminary tests (distribution visualization, residual histogram, overdispersion test) indicated that the 'Poisson' family was the most suitable for this model. The selection process for these models is the same as described in the previous section (6.2.1).

6.3. Best predictors of crop damage in sugarcane fields

To identify the best predictors of sugarcane damage, we compared multiple candidate models using linear mixed-effects models with the *lmer* function from the *lme4* package, after checking model residuals using the *simulateResiduals()* function to validate model assumptions. Each model included the number of damages recorded in the quadrat (i.e., the total number of sugarcane stems eaten) as the response variable and one independent variable: either the number of CFEs recorded every 15 days, the number of individuals feeding, or the total duration of CFEs. The fortnightly frequency was chosen to align with the damage assessments, which were also conducted every 15 days. Including these variables in the same model was not feasible due to collinearity.

To model for site-specific variability, the variable 'Site' was included as a random effect in each model. The models provided accurate and reliable estimates, justifying the use of random effects in this context (Oberpriller et al., 2022). Nakagawa's R^2 , which quantifies the proportion of variance explained by both fixed and random effects, was calculated for each model, and marginal R^2 was used to select the best model. Model comparison was based on the Akaike Information Criterion corrected for small sample sizes (AICc), using the *MuMin* package. The model with the lowest AICc value and the highest R^2 was selected as the best model.

6.4. Questionnaire survey

6.4.1. *Assessing attitudes toward macaques*

To estimate the respondents' overall perceptions and attitudes toward macaques, we initially analyzed these perceptions in terms of positive, negative, or neutral values. We first selected the questions to which we could assign one of these three values (Q12, Q13, Q14, Q15, Q17,

Q19, Q20, Q21, Q39, Q40, Q43, Appendix 2). We attributed a score ranging between -1 and 1 to each response item in the questionnaire. The negative, null and positive absolute values referred to negative, neutral and positive attitudes, respectively. Positive values primarily referred to perceptions or attitudes that were positive or tolerant toward macaques (e.g., Considering macaques as sacred, accepting them taking a small portion of the harvest), while negative values referred to perceptions or attitudes that were negative or conflictual (e.g., Considering macaques as dangerous or hunting them). Neutral values referred to perceptions or attitudes that were neutral toward macaques (e.g., No perceived change or lack of opinion). We calculated the proportion of positive, neutral, and negative attitudes and perceptions in the questionnaire to identify the overall proportions of perceptions on the island. Informations on macaque crop-feeding behavior and attitudes toward trapping were analyzed descriptively.

6.4.2. *The role of socio-cultural variables in local attitudes*

Then, we aimed to determine whether socio-cultural variables influenced perceptions and attitudes towards macaques. We selected the following items in the questionnaire as perceptions or attitudes to analyze: (a) Presence/absence of the perception of macaques as: i. Sacred (Q17); ii. Beneficial (Q19); iii. Dangerous (Q21). (c) Presence/absence of the perception of an increase in: i. Conflict over the past 30 years (Q36); ii. Aggressiveness compared to before (Q13). (d) Presence/absence of preference for: i. More monkeys being trapped (Q43) (Annexe 1). These items were treated as binary response variables (yes/no) in the model. Responses 'do not know' or 'refusal' were considered as missing values in the analysis. We then conducted logistic regression analyses (GLM with a binomial family and logit link function) to evaluate the influence of socio-cultural variables (categorical predictors) on the respondents' perception/attitude. Given the relatively small sample size ($N = 55$), we restricted the number of predictors in the models to the most relevant ones, based on our study objectives. Specifically, we included the following predictors: age (i.e., Young < 41 years old vs. Old ≥ 41 years old), education level (i.e., Low level up to primary vs. Higher level from secondary), and religion (i.e., Hindu vs. Other religions).

We run the logistic regression models with the Matrix and *lme4* packages in R. To identify the best model for each response variable, we employed the dredge function from the *MuMin* package, and selected the best models using the AICc. We systematically checked the assumptions of the logistic regression models, including multicollinearity (assessed with VIF) and overdispersion

III. RESULTS

1. General results

1.1. CFE parameters

A total of 776 macaque videos were collected, and 193 CFEs were recorded across all study sites. On average a CFE lasted 14 ± 18.67 minutes (range: min = 1; max = 72), and there was no significant difference between study sites (Kruskal-Wallis test, $\chi^2 = 6.133$, $df = 5$, $p = 0.293$). Most CFEs (61%) lasted 1 to 10 minutes in duration (Figure 7a).

Regarding the number of macaque individuals involved, there was on average 2 individuals per CFE (range: min = 1; max = 17) and there were no significant differences across sites (Kruskal-Wallis test, $\chi^2 = 9.925$, $df = 5$, $p\text{-value} = 0.077$). Most CFEs (64%) involved three or fewer individuals and 24% involved more than five individuals (Figure 7b).

CFEs by single individuals were significantly shorter than those involving groups of two or more individuals (Wilcoxon test, $\bar{x}_{\text{single}} = 3.26$, $\bar{x}_{\text{multiple}} = 18.34$, $W = 2797.5$, $p < 0.001$). Details about CFE parameters can be found in Table 3.

Table 3. Parameters of Crop Feeding Events (CFEs) across sites: relative frequency, rate per weeks, average duration, and average number of individuals per CFE (Standard Deviation in parentheses).

Site	CFEs daily frequency ¹	CFE mean duration	Mean no. of individual per CFE ²
Alteo 1	0.30	16.5 ± 20.4	4.13 ± 7.07
Alteo 2	0.67	15.3 ± 19.1	2.53 ± 2.50
Medine 1	0.37	15.51 ± 17.5	4.59 ± 5.15
Medine 2	0.34	14.5 ± 22.0	2.18 ± 3.50
Bellevue	0.23	13.2 ± 14.9	6.21 ± 5.48
Plaine Sophie	0.32	5.6 ± 9.76	1.80 ± 1.28

¹The daily frequency of CFEs was calculated as the total number of CFEs divided by the number of camera-days at each site.

²“no.” refers to “Number”.

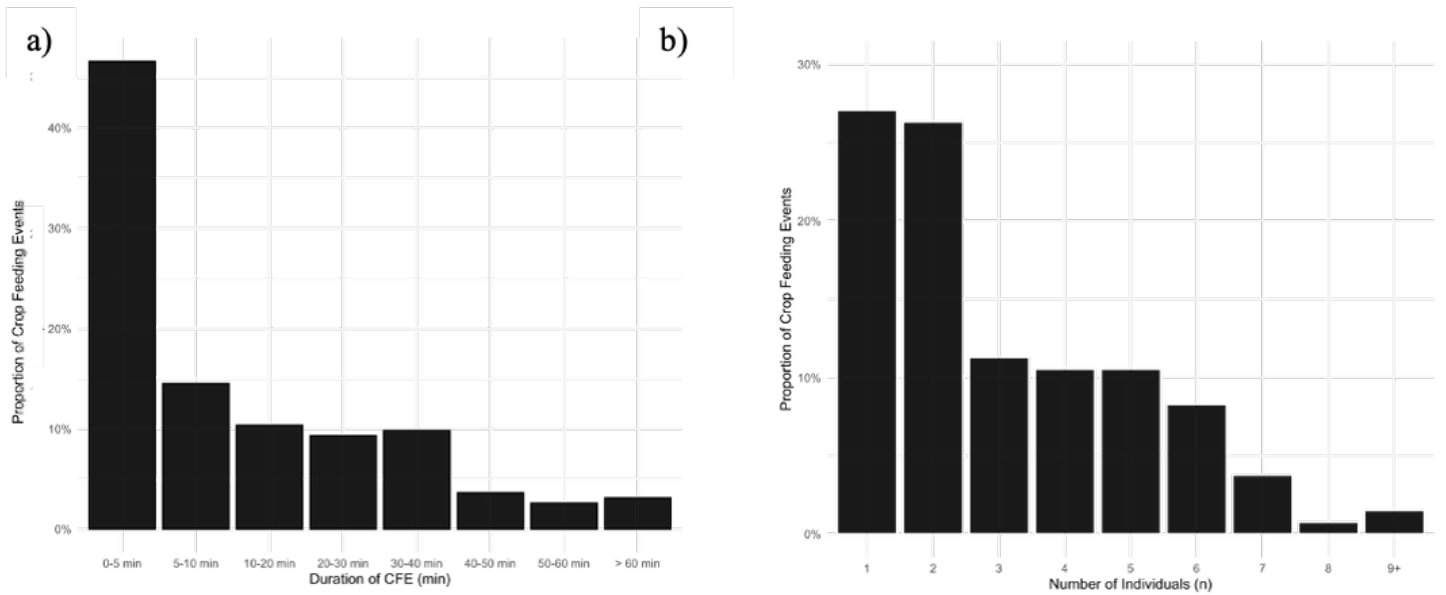


Figure 7. a) Proportion of CFEs durations and (b) feeding group sizes across all sites (CFEs = 193).

1.2. Temporal patterns

Crop feeding events occurred throughout the day (06:00 am–06:00 pm) (Figure 8). However, the average number of CFEs was highest between 3:00-6:00 pm ($n_{\text{sugarcanes}} = 42$; $n_{\text{vegetables}} = 19$) and lowest between 6:00-9:00 am ($n_{\text{sugarcanes}} = 35$; $n_{\text{vegetables}} = 2$) across both vegetable and sugarcane crops.

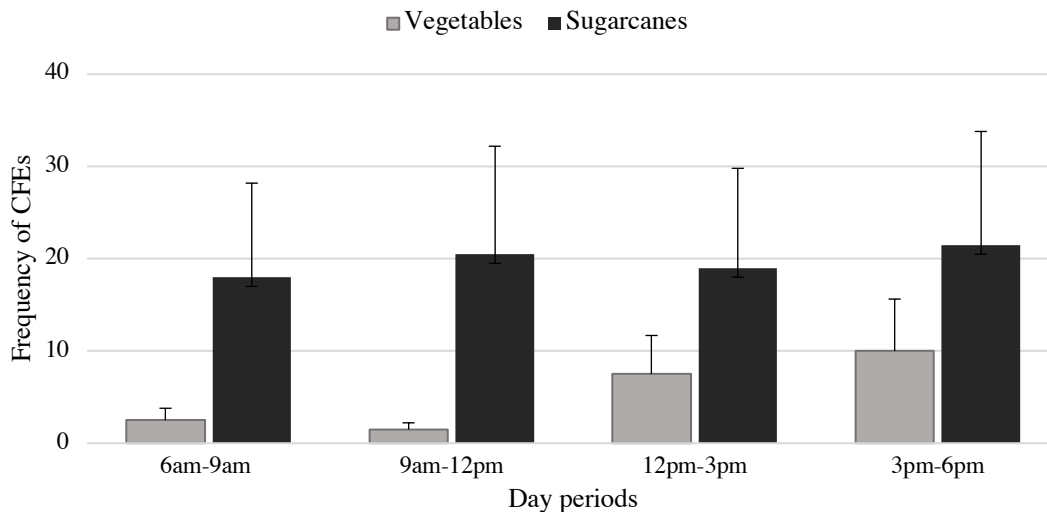


Figure 8. Frequency of crop feeding events (CFEs) with standard deviation by macaques in sugarcane and vegetable crops for each time period of the day.

For sugarcane fields, we did not find any significant differences in the distribution of CFEs across time periods (Chi-square test, $\chi^2 = 0.75$, $df = 3$, $p > 0.05$), suggesting that the frequency

of CFEs remains relatively uniform throughout the day. However, for vegetable fields, we did observe a significant difference in the distribution of CFEs across time periods (Chi-square test, $\chi^2 = 20.18$, $df = 3$, $p < 0.001$), suggesting that macaques exhibit distinct feeding behaviors at different times of the day in these crops. The pairwise comparisons revealed significant differences between the "3pm-6pm" and "9am-12am" periods ($p < 0.01$), as well as between "3pm-6pm" and "6am-9am" ($p < 0.01$). No significant differences were found between "12pm-3pm" and other periods (Figure 8).

In vegetable fields, humans predominantly visited during the morning (83% of visits), whereas macaques exhibited the opposite pattern (Figure 9), with most visits occurring in the afternoon (82%) compared to the morning (18%). In sugarcane fields, the differences were less pronounced for both species. Humans visited slightly more in the morning (54%) than in the afternoon (46%), while macaque visits were slightly higher in the afternoon (55%) compared to the morning (45%). The chi-square test revealed significant differences in the distribution of visits between morning (6 am–12 pm) and afternoon (12 pm–6 pm) for macaques and humans in both vegetable fields (Chi-square test, $\chi^2 = 102.52$, $df = 1$, $p\text{-value} < 0.001$) and sugarcane fields (Chi-square test, $\chi^2 = 6.264$, $df = 1$, $p\text{-value} = 0.01$).

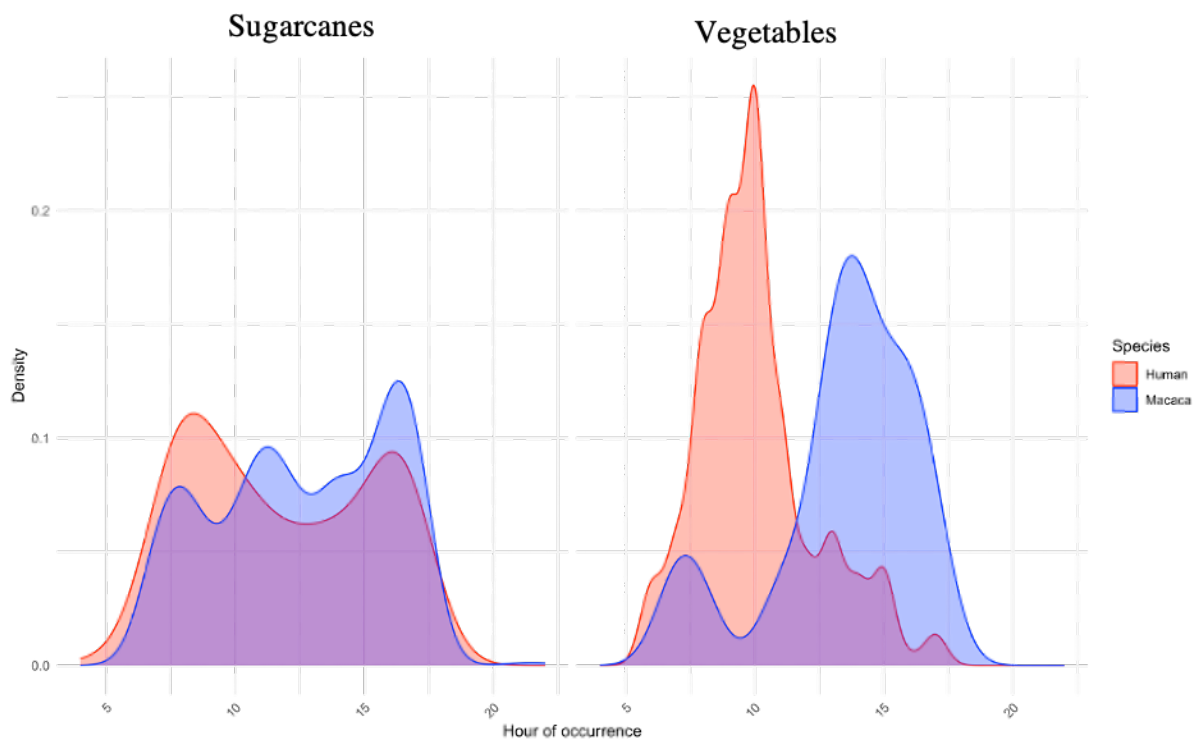


Figure 9. Density of occurrence times by species and crop type. The density curve visually represents the distribution of occurrence times for both groups (human vs macaque).

2. Effect of temporal, spatial and demographic characteristics on CFE duration

2.1. Most influential predictors explaining variation in CFE duration

We found that several factors significantly influence the duration of crop feeding events (CFEs) by macaques (Table 4, Figure 10, Figure 11). Among these, demographic parameters emerged as the most influential. Specifically, the total number of individuals involved in CFEs and the proportion of adults both had a significant positive effect on foraging duration. Larger group sizes or a higher proportion of adults were associated with longer foraging events (Table 4).

Conversely, the proportion of forest and farmland were negatively associated with foraging duration, suggesting that a higher proportion of surrounding forest and farmland are associated with shorter CFEs. However, contrary to our predictions, the distance to buildings did not significantly affect the foraging duration, implying that proximity to human infrastructures had no influence on macaque foraging behavior.

Table 4. Raw and adjusted P-values of the likelihood ratio tests between the global model explaining variation in CFE duration and the reduced models in which one of the five predictors was dropped. For the predictors that were included in the final model, the regression estimates with their standard errors (SEs) and 95% confidence intervals (CI_{low} , CI_{up}) have also been provided.

Predictors	P_{raw}	$P_{adjusted}$	Included in final model	Estimate \pm SE (CI_{low} , CI_{up})
Total individuals feeding	<0.001	<0.001	Yes	0.07 \pm 0.01 (0.06, 0.09)
Proportion of adults	< 0.05	< 0.05	Yes	0.26 \pm 0.13 (0.01, 0.51)
Proportion of forest	<0.001	<0.001	Yes	-2.39 \pm 1.18 (-4.69, -0.08)
Proportion of farmland	<0.001	<0.001	Yes	-2.24 \pm 1.15 (-4.5, 0.01)

Based on our results and to ease the interpretation of these results, the graphical representations of all predictors are provided below (Figure 10, 11).

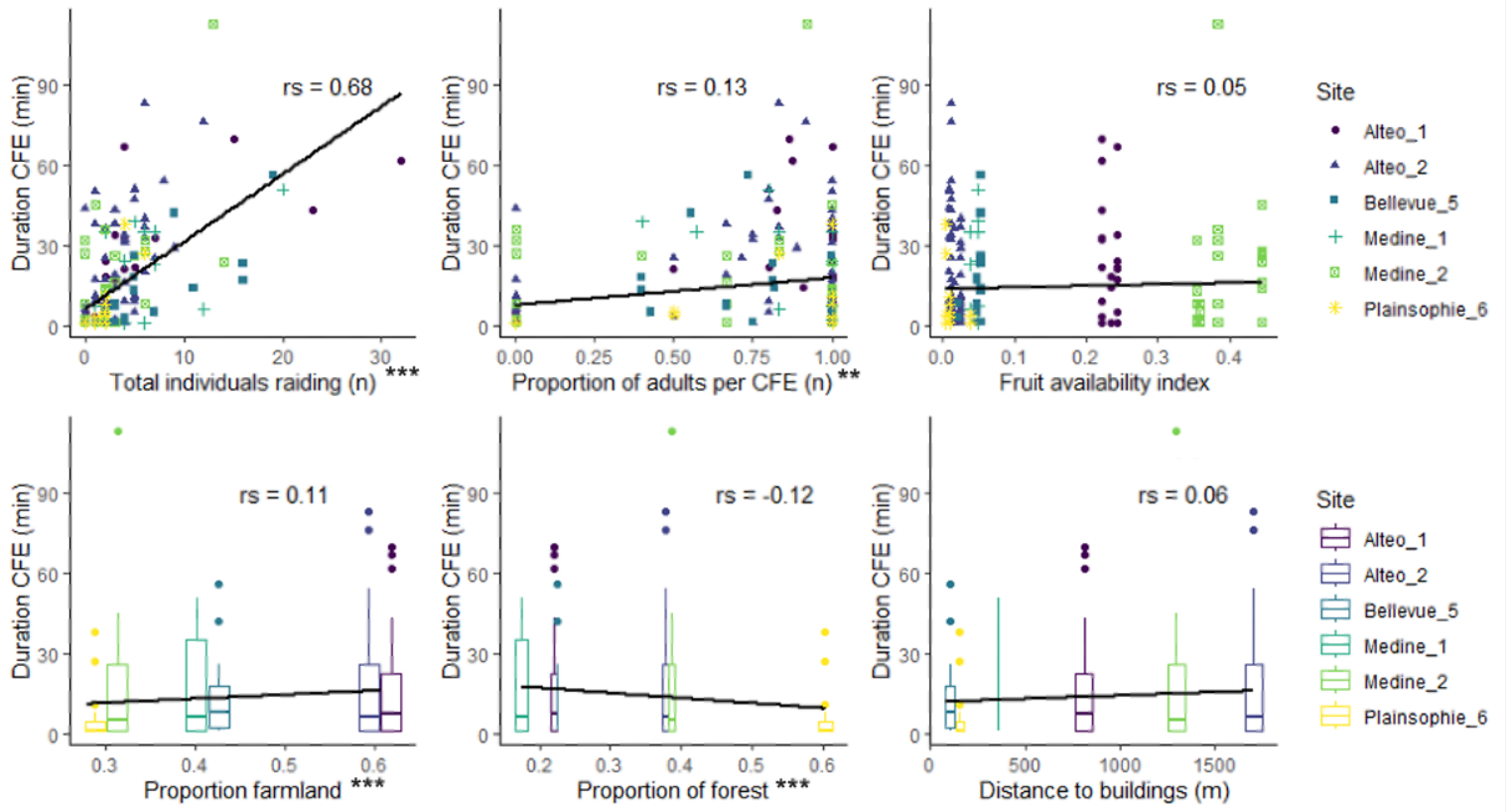


Figure 10. Each predictor plotted against the duration of crop feeding events (duration CFE) with a line of best fit estimated by a simple linear regression to illustrate the direction of each relationship. Observations from different sites (Alteo 1, Alteo 2, Bellevue, Medine 1, Medine 2 and Plaine Sophie) have been highlighted in different shapes and colors. For proportion farmland, proportion of forest and distance to buildings we have added boxplots instead of single observations, as these predictors only have a single value per site. Spearman's (rs) correlation coefficients have also been added to each plot. All predictors with $rs > 0.1$ were included in our final Generalized Linear Model.

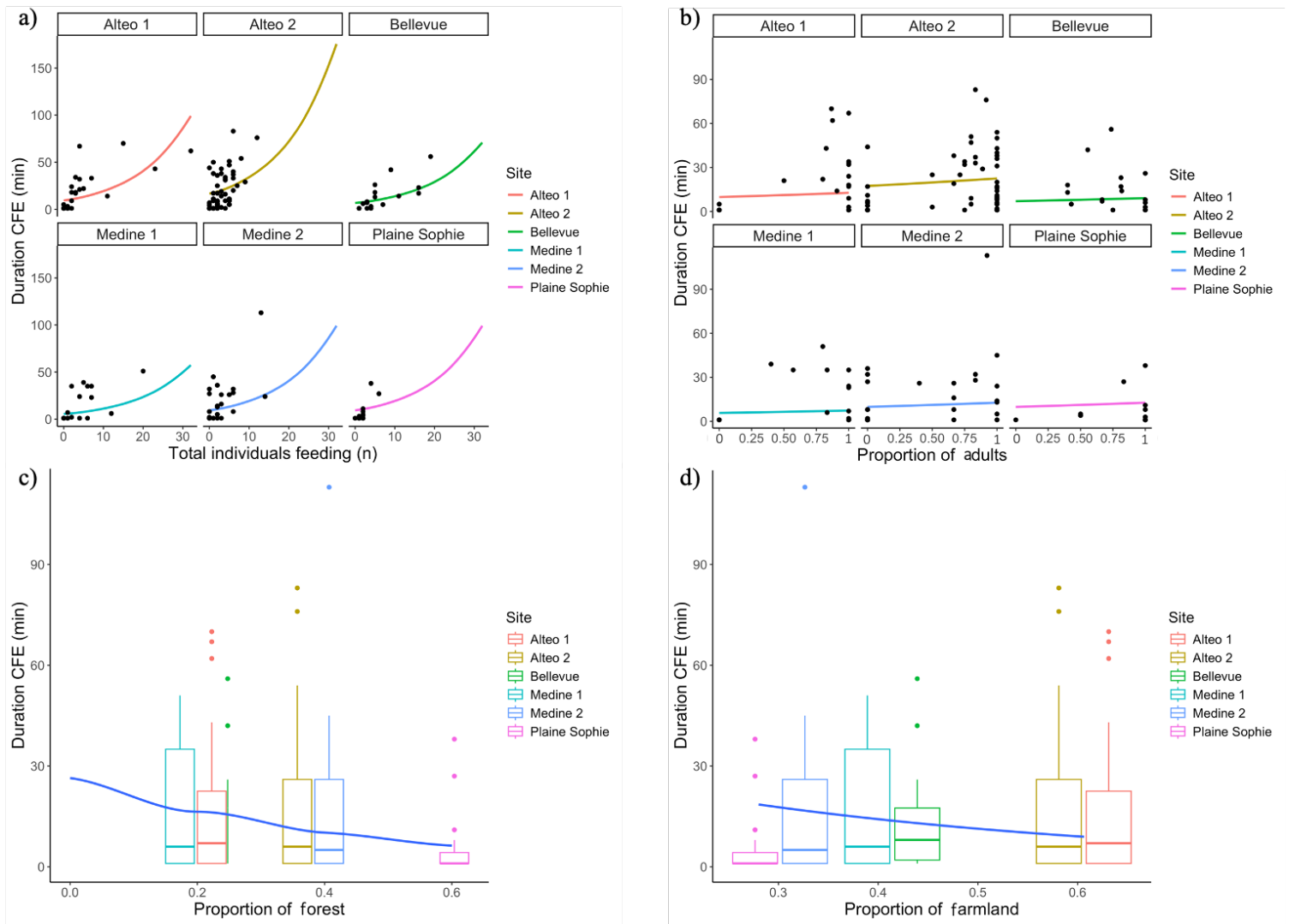


Figure 11. Lines of best fit estimated by our two Generalized Linear Mixed Models (GLMMs) expressing the relationship between the duration of crop feeding events (Duration CFE) and a) the total number of individuals, b) the proportion of adults, c) the proportion of forest, and d) the proportion of farmland in each site. For proportion of forest and proportion of farmland boxplots were added instead of single observations, as these predictors only have a single value per site.

2.2. Most influential predictors explaining variation in weekly CFE frequency

We found that several factors influenced the frequency of weekly crop feeding events by macaques (Table 5, Figure 12, Figure 13). The proportion of adult macaques had a significant positive effect on the frequency of CFEs, with a greater proportion of adults leading to more frequent foraging. Additionally, the number of weeks since the start of the study is negatively associated with CFE frequency, suggesting that as time progresses, macaques forage less frequently (Table 5).

The proportion of forest, proportion of farmland, distance to buildings, and fruit availability index did not significantly influence the frequency of CFE ($p > 0.05$ for all), indicating that these factors are not as relevant for determining the frequency of macaque foraging events. To ease the interpretation of these results, the graphical representations of the effects of these predictors are provided below (Figure 12, 13).

Table 5. Raw and adjusted P-values of the likelihood ratio tests between the global model explaining variation in weekly crop feeding event (CFE) frequency and the reduced models in which one of the seven plausible predictors was dropped. For the predictors that were included in the final model, the regression estimates with their standard errors (SEs) and 95% confidence intervals (CI_{low} , CI_{up}) have also been provided.

Predictors	P_{raw}	$P_{adjusted}$	MSE	Included in final model	Estimate SE (CI_{low} , CI_{up})
Proportion of adults	<0.001	< 0.001	8.61	Yes	1.43 ± 0.32 (0.7, 2.07)
Weeks since start of study	< 0.05	< 0.05	8.53	Yes	-0.07 ± 0.02 (-0.09, -0.01)
Proportion of farmland	> 0.05	> 0.05	8.46	No	-
Distance to buildings	> 0.05	> 0.05	8.46	No	-
Fruit availability index	> 0.05	> 0.05	8.47	No	-

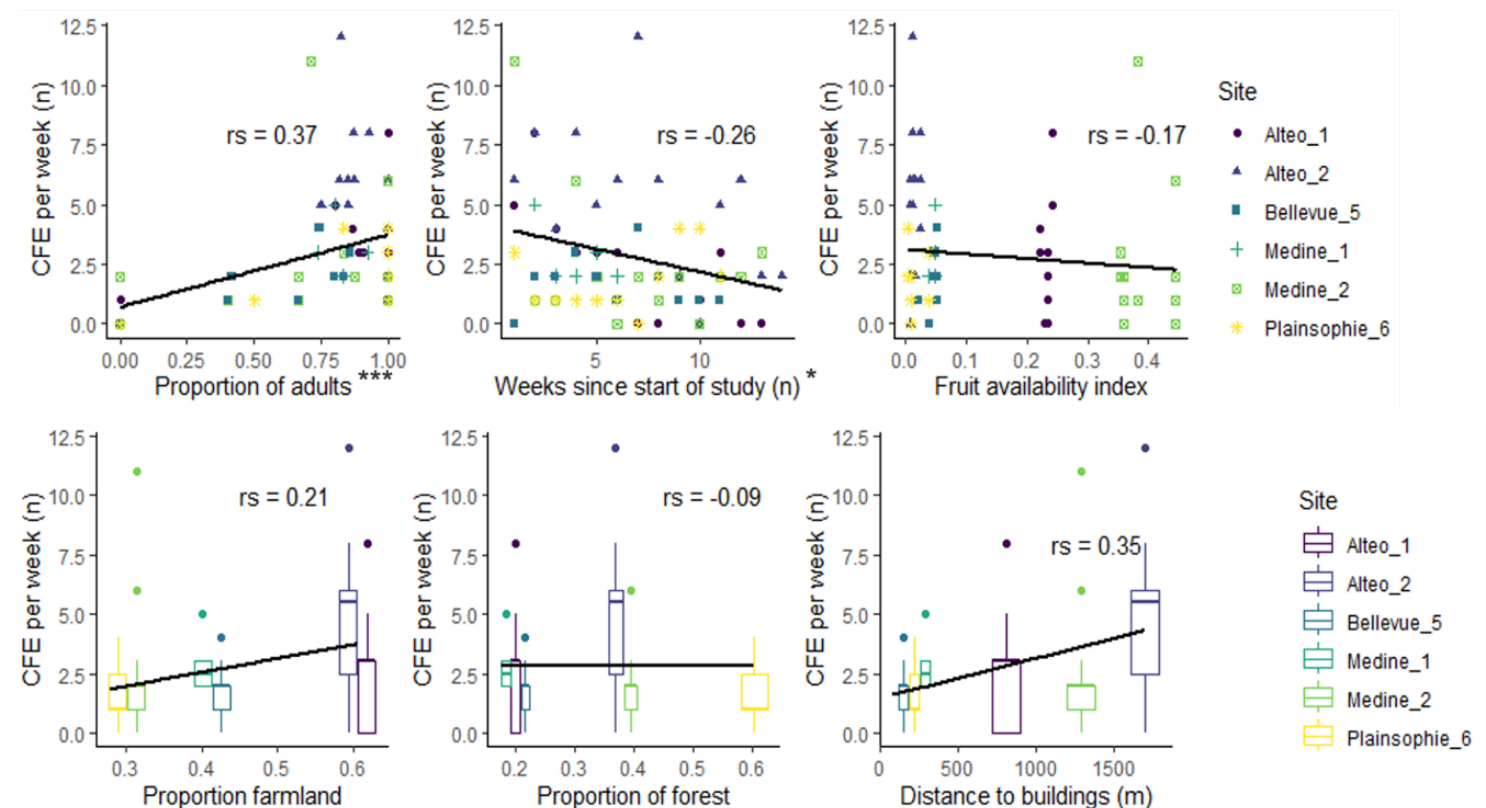


Figure 12. Each potential predictor plotted against the number of crops feeding events (CFE frequency per week) with a line of best fit estimated by a simple linear regression to illustrate the direction of each

relationship. Observations from different sites (Alteo 1, Alteo 2, Bellevue, Medine 1, Medine 2 and Plaine Sophie) have been highlighted in different shapes and colors. For proportion farmland, proportion of forest and distance to buildings we have added boxplots instead of single observations, as these predictors only have a single value per site. Pearson's (r) and Spearman's (rs) correlation coefficients have also been added to each plot. All predictors with $r_s > 0.1$ were included in our final Generalized Linear Model

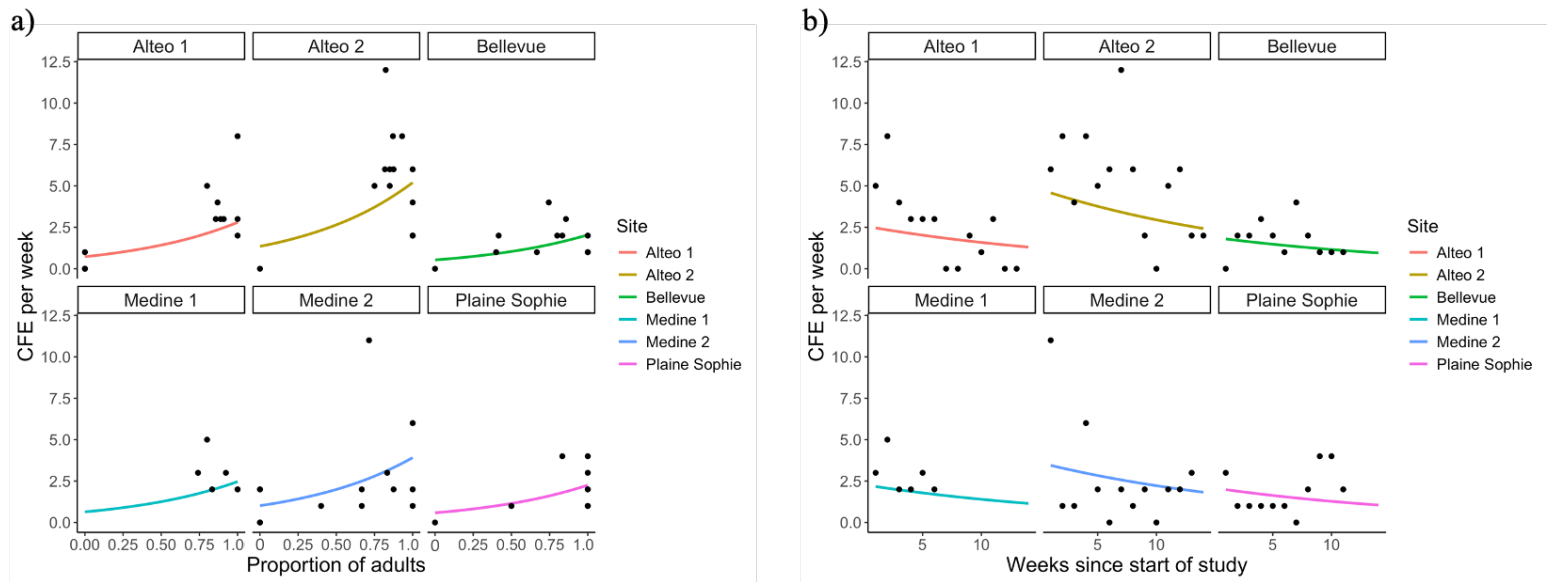


Figure 13. Lines of best fit estimated by our two Generalized Linear Mixed Models (GLMMs) expressing the relationship between the CFE frequency (CFE per week) and (a) the proportion of adults and (b) the weeks since the start of the study.

3. Best predictor of damage to sugarcane crops

3.1. Best predictor of damages to sugarcanes

As a reminder, our goal was to determine which of the three predictors—number of individuals, duration or total frequency of CFEs —best explained the observed damage in the sugarcane fields. We found that each variable significantly predicted the extent of damage, although their explanatory power and relative importance varied (Table 6, 7, Appendix 5).

Contrary to our expectations we found that the number of CFEs was the most influential predictor, with each additional visit increasing the average damage by 2.56 units per quadrat ($p < 0.001$). This predictor explained 60% of the variance and had 94.9% probability of being the best model among those compared according to the AICc criteria (Table 7). In contrast, the total number of individuals involved in CFEs positively influenced damage, with more individuals causing greater damage. This factor explained 56% of the variation but received

less support compared to other variables (Table 7). Similarly, the duration of CFEs had a positive effect, with longer durations leading to increased damage, explaining 52% of the variation and receiving the least support (Table 7).

Table 6. Results of the mixed linear model predicting sugarcane damage based on the duration, total frequency of CFEs and number of individuals. The table shows estimated coefficients (Estimate), standard errors (Std Error), t-values (t-value), and p-values (Pr(>|z|)) for the intercept and predictor variable.

Predictor	Estimate	Std Error	t-value	Pr(> z)
Damage ~ Number of CFEs	2.562	0.422	6.078	< 0.001
Damage ~ Number of individuals	0.654	0.125	5.219	< 0.001
Damage ~ Duration of CFEs	0.121	0.021	5.682	< 0.001

Table 7. Model comparison based on Marginal R², k, ΔAICc and Akaike weight (ω) to evaluate predictors of sugarcane damage.

Ranked models	Marginal R²	k	ΔAICc	ω
Damage ~ Number of CFEs	0.609	4	0.00	0.949
Damage ~ Number of individuals	0.562	4	6.8	0.032
Damage ~ Duration CFEs	0.524	4	7.8	0.019

An illustration of the results for each predictor is provided in Appendix 5.

4. Opinions of farmers towards macaques

4.1. General attitudes and perceptions of farmers towards macaques

Our last objective was to assess the general attitude and perception of farmers toward macaques. We differentiated between perceptions and self-reported behaviors toward macaques and we found that the average scores of the respondents toward macaques were nuanced. Regarding perceptions, forty-three percent of respondents viewed macaques negatively, 33% held a positive perception, and 24% remained neutral (Figure 14a). The average score for behaviors was completely different, with 74% of respondents showing positive behaviors toward macaques, 22% negative, and 9% neutral (Figure 14b).

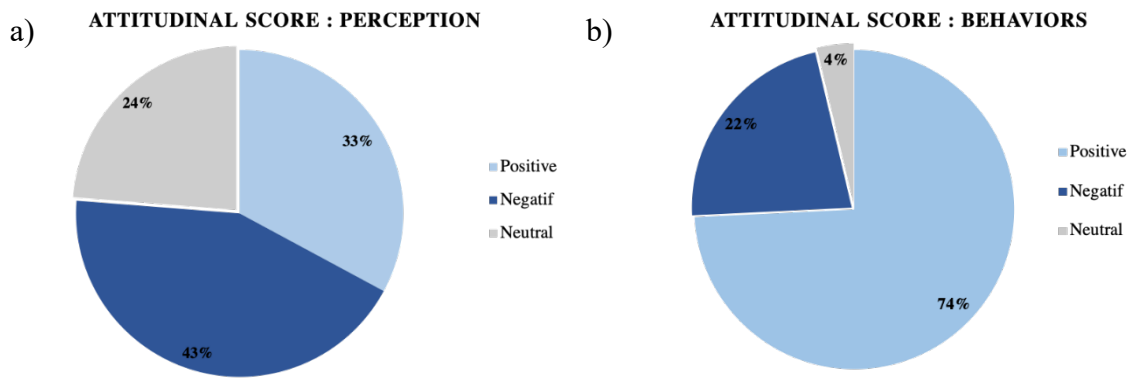


Figure 14. Average scores of a) perceptions and b) self-reported behaviors of respondents (local farmers) towards macaques in Mauritius

These descriptive results indicated that farmers generally held negative perceptions of macaques. Specifically, 60% of respondents perceived them as dangerous, and 50% saw no benefit to their presence on the island. Additionally, 41% of farmers reported feeling negative emotions when seeing a macaque, 39% expressed neutrality, and only 20% reported positive emotions. The perception of macaques as sacred was evenly split, with an additional 13% remaining neutral on the subject. However, interestingly, the majority of respondents displayed positive self-reported behaviors toward macaques. For instance, 92% stated they had never hunted or consumed macaques, and 35% were willing to tolerate macaques feeding on their crops and taking a small portion.

When examining the role of religion (Figure 15), attitudes toward macaques were noticeably more positive among Hindus (51%) compared to individuals of other religious affiliations. For instance, nearly 60% of Hindus expressed that they did not want macaques to disappear from Mauritius. Similarly, 45% of Hindus were willing to allow macaques to take a portion of their crops. In contrast, more than half of non-Hindus favored the complete eradication of macaques, with only 11% willing to share a portion of their harvest.

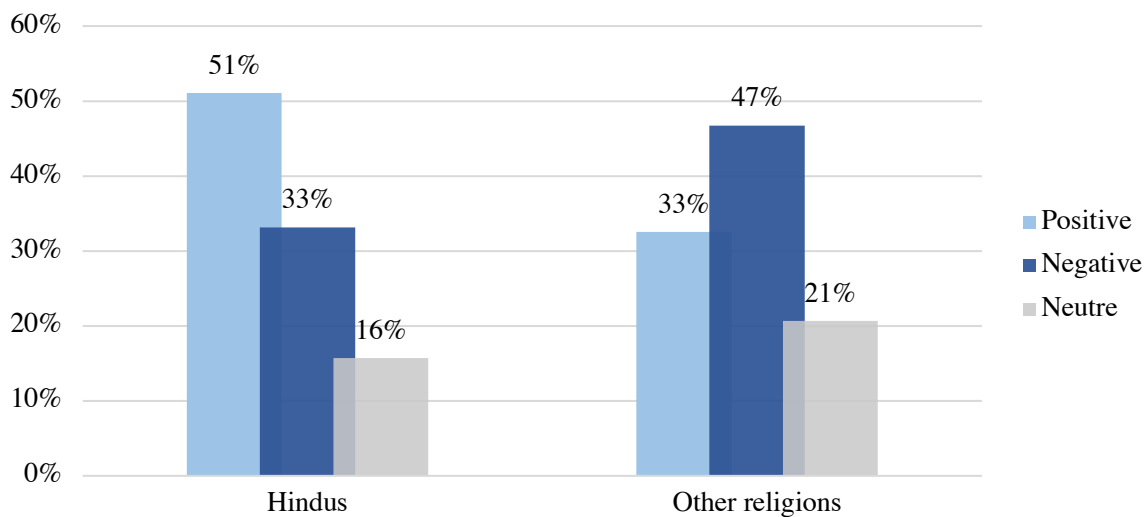


Figure 15. Comparison of the nature of attitudinal scores (Positive, Negative, Neutral) toward macaques between Hindu and other religions.

4.2. Nuisance and attitudes towards trapping

Among all respondents, 81% reported a significant general increase in macaque crop feeding activity in the last ten years, and 75% said that macaques came to their farms every day. Regarding their crop loss estimates due to macaques, 16% reported losing more than 50% of their crops, while 32% reported losing less than 10%.

For repellents, the majority of farmers (50%) used firecrackers. Sixteen percent simply shouted or threw stones, and 14% did nothing at all. Only one farmer used guards to protect its fields, paying them for this service (**Annexe 3**). Regarding trapping, more than 62% of respondents supported the installation of traps near their homes. 31% ($n = 17$) reported having traps near their properties. Of those with traps, 56% found them effective in reducing crop feeding, while 31% considered them ineffective.

4.3. Influence of socio-cultural variables

4.3.1. Perception of sacredness

The perception of macaques as sacred was influenced by two socio-cultural variables: religion and age. Logistic regression results showed that non-Hindu farmers (i.e., Muslims and Christians) were significantly less likely to perceive macaques as sacred compared to Hindu farmers (Estimate \pm SE = -1.395 ± 0.687 , $p = 0.04$). Regarding age, older farmers (over 41 years old) were also less likely to hold this perception, although the trend was only marginally significant (Estimate \pm SE = -0.960 ± 0.631 , $p = 0.07$).

4.3.2. *Perception of macaque presence in Mauritius*

When it comes to seeing the presence of macaques as beneficial (or not) to the island, perceptions varied by education level. Farmers with lower levels of education ("Low Education") were significantly less likely to consider macaques as advantageous (Estimate \pm SE = -1.655 ± 0.829 , $p = 0.04$).

4.3.3. *Support for capturing macaques*

We found that support for macaque capture was influenced by age. Farmers older than 41 years were significantly more likely to support increased capture of macaques around their fields (Estimate \pm SE = 1.743 ± 0.832 , $p = 0.03$).

4.3.4. *Support for the total elimination of macaques*

Regarding the scenario of a total elimination of macaques in Mauritius, no variable showed a statistically significant effect. However, there was a trend suggesting that non-Hindu respondents were more likely to support total elimination compared to Hindu respondents (Estimate \pm SE = 1.143 ± 0.676 , $p = 0.08$).

4.3.5. *Perception of increasing crop feeding, danger and increase in aggressiveness of macaques*

Although most of the respondents (81%) reported an increase in crop feeding by macaques over the past ten years, no socio-cultural variables significantly explained this perception. Similarly, 60% considered macaques dangerous, but no socio-cultural factors were significant in this regard either. Regarding macaque aggressiveness, opinions were more divided: 31% thought macaques had become more aggressive, 29% believed they had become less aggressive, and 38% saw no change. However, no socio-cultural variables explained these differences.

IV. DISCUSSION

This study is, to our knowledge, the first to examine human-long-tailed macaque interactions regarding crop feeding in Mauritius and represents an initial effort in mitigating macaque-related crop damage. We aimed to address this problematic through three main objectives: (a) to examine the influence of spatial, temporal, and demographic factors on macaque crop feeding patterns; (b) to estimate key crop feeding parameters, including frequency, duration, and the number of individuals involved, as indicators of crop damage in each field – using the count of crop items removed by macaques as a proxy for damage – and (c) to explore farmers' perceptions of macaques in areas significantly affected by crop foraging. To achieve these objectives, we adopted a multidisciplinary approach that integrated animal and human perspectives.

What are the characteristics and temporal distribution of CFEs?

The duration of visits to the fields by macaques is similar to previous observations in rhesus macaques (*Macaca mulatta*) foraging in agricultural fields in India, where the duration was also approximately 14 minutes (Anand & Radhakrishna, 2022). However, our results also revealed considerable variability in CFEs duration. While the majority of CFEs lasted less than 10 minutes, some extended beyond an hour (Fig. 7a). The literature similarly highlights the absence of a uniform pattern in CFEs duration in primates. For instance, southern pig-tailed macaques (*M. nemestrina*) have been observed visiting oil palm plantations for over three hours (Holzner, 2021), whereas chacma baboons (*Papio hamadryas ursinus*) seldom stayed longer than three minutes in graminoid fields (Schweitzer et al., 2017). These discrepancies highlight the influence of multiple factors on crop feeding behavior, emphasizing the importance of conducting location-specific studies across species to better understand these dynamics.

In addition, the frequent presence of small groups or solitary macaques we found in our fields is consistent with former studies. A general trend among primates foraging on crops is the tendency to form smaller groups for foraging (cf. foraging parties) compared to their overall group size (Wallace & Hill, 2012; Warren et al., 2007). This strategy of foraging in smaller parties helps reduce visibility (Forthman-Quick & Demment, 1988), lowers the chances of being spotted by farmers, and minimizes potential risks.

When considering the daily temporal pattern of CFEs, contrary to our expectation, our results suggested a consistent presence of macaques throughout the day in sugarcane. Additionally, we found that the difference in the distribution of visits between morning and afternoon was

minor between human and macaque, further illustrated by a big overlap in their occurrence of visit across the day (Figure). This suggests that macaques' crop-feeding behavior in sugarcane fields may be less influenced by human presence.

This finding deviates from previous studies that report distinct temporal patterns in crop feeding behavior. For instance, Sumatran orangutans (*Pongo abelii*) living in agroforests altered their feeding behavior to forage predominantly in the late afternoon or evening, after farmers had left the fields. In Mauritius, Bernstein (1968) reported that long-tailed macaques have been observed restricting their crop foraging activity in sugarcane fields to early morning or late evening, particularly when human guards were absent. In contrast, our findings would suggest that sugarcane fields provide a relatively low-risk foraging environment for macaques. This may be attributed to the limited human presence throughout the day as sugarcane fields in the study area are not actively monitored. Breeders occasionally visited to set traps, but macaques don't actively monitor them. Apart from occasional human or vehicular activity, there was no continuous presence, further lowering the macaques' perception of risk. Additionally, the limited number of people passing through the fields means they may not actively chase macaques when they see them, allowing macaques to temporarily hide and return once the person has passed. Furthermore, we observed some macaques' sleeping sites in close proximity to sugarcane fields which supports the idea that they may prioritize maximizing energetic gains while minimizing perceived risks by foraging near their resting sites. In their study, Brotcorne et al (2014) found that *M. fascicularis* preferentially selected sleeping trees situated within or near human-modified zones, particularly when anthropogenic food was abundant, natural food resources were limited, and the risk of predation was low.

Conversely, we found a contrasting foraging pattern in vegetable fields, where macaques were more likely to forage in the afternoon, as human activity was overwhelmingly concentrated in the morning. Although we never observed macaques being explicitly chased by farmers on the camera traps, discussions with the farmers suggested that they all actively chased the macaques whenever they saw them entering in the vegetable fields. The smaller field sizes would allow farmers to monitor the entire perimeter more effectively. Additionally, small-scale farmers would depend on their harvest for income, unlike sugarcane workers who would receive a salary regardless of crop losses (Dillon & Dambro, 2017). This may result in more frequent negative interactions, heightened risk perception, and potentially increased avoidance behavior by Mauritius macaques in vegetable fields.

Is the frequency and duration of CFEs influenced by demographic, spatial or temporal patterns?

Demographic patterns: Our investigation aimed to identify factors influencing crop feeding activity and revealed that demographic variables, particularly the number of individuals and the proportion of adults present, were important predictors of CFEs duration. Specifically, we found convincing evidence that the total number of individuals per CFE increased CFEs duration. Baboons and chimpanzees exhibit similar patterns across different group sizes (Wallace & Hill, 2012) and in Buton macaques (*M. ochreata brunnescens*) CFE duration also increases with group size (Priston et al., 2012).

While only few studies investigated this specific question, some research on group foraging dynamics in natural context provides valuable framework for understanding how group dynamics can influence foraging behavior. For instance, we know that across species, the presence of conspecifics in a group decreases individual vigilance for predators, allowing for an increase in time allocated to foraging activities (Hamilton, 1971; Powell, 1974; Lima & Dill, 1990). When applied to crop foraging behavior, an inherently risky activity (Hill, 2017), larger group sizes likely increase risk perception, potentially leading to longer foraging events. This aligns with studies on primate foraging in high-risk environments, where animals form larger groups in response to increased predation risks (Hill & Lee, 1998).

Our findings suggest that CFEs duration and weekly frequency were positively associated with the proportion of adults. The fact that crop feeding behavior is adult-led and adult-oriented activity has been found in five different primate species in the study of Wallace & Hill (2012) and in several studies on macaques (Priston, 2005; Priston et al., 2012, Anand & Radhakrishna, 2022). Adults are more experienced and efficient at foraging and they may be more involved in prolonged feeding bouts (Schweitzer et al., 2017; Hill, 2017). Furthermore, studies on group coordination and collective decision-making in primates have shown that highly affiliated individuals are more likely to be followed during group movements (A. J. King & Sueur, 2011). Compared to immatures, adults often hold central roles in social network and dominance hierarchies, and possess greater affiliative bonds within the group. Therefore, they are more likely to lead and sustain crop-foraging events. This leadership role may not only contribute to the longer duration of CFEs but may also encourage increased participation from other group members and more frequent intrusions in the field (Priston et al., 2012).

In regions where primates are trapped for biomedical research, such as China and Cambodia, females are primarily targeted for their reproductive capacity. Only a few males are needed, while many females are required to produce offspring (Warne et al., 2023). A similar

trend has been noted in Mauritius (Florens, 2022), and this pattern was further confirmed by reports from several farmers and landowners interviewed in this study. This may create a demographic bias in the sex ratio, with a disproportionate number of males in groups compared to females in the wild. Such a demographic shift could potentially exacerbate crop foraging frequencies, as males are more frequently involved in CFEs (Hill, 2017; Schweitzer et al., 2017; Strum, 2010). The lack of detailed information on trapping practices in the vicinity of our study sites may have limited our ability to fully evaluate its impact on the observed foraging patterns. We strongly recommend that future research collaborates closely with trappers and wildlife management authorities to gather comprehensive data on trapping practices. Such collaborations are essential for assessing the long-term consequences of selective trapping on group demographics, population dynamics, and their subsequent effects on crop foraging patterns.

Temporal patterns: Regarding temporal patterns, we found no significant differences in either the frequency or duration of CFEs relative to natural fruit availability in the forest. However, we found that macaques engaged in less crop feeding in sites with larger forest cover. This suggests they may spend more time in forested areas with sufficient natural food, thereby reducing their reliance on crops, a pattern consistent with findings from other primate studies (Hockings et al., 2009; Naughton-Treves et al., 1998) including *M. fascicularis* (Brotcorne, 2014). The lack of a significant correlation with fruit availability could be explained by the relatively short duration of the phenological survey, which spanned only four months, primarily during the dry season, and concluded just before the onset of the wet season. This latter period is typically marked by an increase in fruit availability, including species like *Litsea glutinosa* and *Psidium cattleianum*, which are highly preferred food sources for macaques (Reinegger et al., 2023). Supporting this hypothesis, we found that macaques' visits to fields decreased over time at all sites, further suggesting a temporal trend potentially influenced by seasonal shifts in resource availability.

A study spanning an entire year, covering both the dry and wet seasons, would be ideal to determine whether crop feeding by macaques is influenced by fluctuations in fruit availability or occurs consistently regardless of the season.

Spatial patterns: Surprisingly and contrary to our hypothesis, a greater proportion of farmland in study sites was associated with shorter CFEs. This finding does not align with previous studies, which often highlight the attractiveness of large and homogeneous cultivated

areas to wildlife able to exploit them (Hockings et al., 2009; Strum, 2010; Koirala et al., 2021). Extensive and uniform cultivated areas can sustain higher food availability, facilitating the maintenance of larger groups of foragers and then longest events of foraging (Naughton-Treves et al., 1998; Strum, 2010). In addition, large patches of easily accessible resources reduce search time, allowing individuals to adopt sit-and-wait foraging strategies (Riley & Priston, 2010; Strum, 2010; Walton et al., 2021), which typically result in extended crop foraging events. The opposite result we found could be due to the wider distribution of agricultural resources, encouraging macaques to move between fields rather than staying in one location for crop foraging. The same pattern was found with African elephants (*Loxodonta Africana*) (Sitati et al., 2005) and baboons in Uganda (Hill, 2000).

However, it is important to point out the uncertainty associated with the effect of spatial variables (cf. large confidence intervals, small effect size) on crop feeding patterns. Additional sites to our study design would help better capture the variability in spatial patterns and their potential key role in predicting the duration or frequency of CFEs. Despite this uncertainty, the analysis confirms that these variables are influential, even if the exact magnitude and direction (for proportion of farmland) require additional data to confirm. It would be valuable to replicate this study across a larger number of fields to confirm the nature of this relationship, if sufficient resources can be acquired.

Furthermore, the small sample size ($N = 6$) and the lack of replicate (one per site) led us to limit the number of predictors in the model. Several confounding factors were not fully accounted for in this study. For example, the number of neighboring crop fields, their crop types, the presence/absence of rivers, and climatic conditions varied significantly across sites, likely influencing macaque behavior and feeding patterns (Link et al., 2010; Torres-Romero et al., 2023; Wallace & Hill, 2012). These limitations call for further investigation, particularly in future studies where a more comprehensive spatial analysis could help controlling for the impact of ecological variables

What are the best predictors of crop damage ?

All key aspects of crop foraging (duration, frequency, and number of individuals) were linked to crop damage. However, contrary to our predictions and previous studies that pointed to the number of individuals as the main factor (Findlay, 2016; Wallace & Hill, 2012), our findings showed that the frequency of CFEs had the biggest impact on crop damage. In addition, no single predictor emerged as overwhelmingly dominant. CFEs frequency accounted

for over 60% of the variance, while the number of individuals explained 56%, and the total duration of CFEs contributed 52%. The fact that crop damage was better explained by the frequency of visits may arise from several interconnected factors. Each additional visit may offer macaques new opportunities to exploit crop resources, leading to cumulative losses even if individual visits result in modest damage. Repeated incursions might also reflect social learning, where primates acquire foraging knowledge through social transmission, thereby increasing the frequency and efficiency of crop foraging behavior (Mitani et al., 2012; Riley, 2007). Additionally, frequent visits may foster growing familiarity with the fields, reducing the perceived risk of human retaliation and encouraging further incursions.

The number of individuals present in the field was also a significant predictor of crop damage: more individuals present during a CFE lead to greater crop damage. Larger groups naturally consume greater quantities of resources collectively and can cover a wider area within a field, increasing the extent of the damage. As previously mentioned, the mechanisms underlying this effect may be attributed to the dilution effect observed in larger groups. Indeed, as group size increases, individual vigilance for predators or humans decreases (Hamilton, 1971), allowing more time and effort to be allocated to foraging and social activities. This enhanced reduced individual risk of predation or retaliation by humans in larger groups likely contributes to more extensive crop damage, as observed in other studies on primates foraging in risky environments (Hill & Lee, 1998). The duration of CFEs, while accounting for a slightly smaller proportion of the variance, is also logically linked to crop damage. Longer foraging events provide primates with more time to consume and damage crops. Moreover, prolonged incursions might lead to greater exploratory behavior, where primates investigate additional areas within fields, thereby increasing the overall impact of a single event.

The finding that crop damage is mainly driven by macaques' visit frequency highlights the importance of deterrents that prevent macaques from entering fields, which would benefit farmers the most. In Mauritius, few farmers actively guard their fields (with humans or dogs). While time-consuming (Hill, 2018), this approach could be an effective deterrent for those who can afford it. Physical barriers such as fencing or natural buffers with non-palatable crops like chili could also restrict access to fields and deter individuals to enter in (Conover, 2002; Honda & Iijima, 2016). However, considering our findings, addressing a single factor may not be enough; effective mitigation requires an integrated approach that explicitly targets all three key parameters: visitation frequency, group size, and the duration of CFEs. For instance, increasing the macaques' perception of risk through visual or auditory deterrents can reduce visitation

frequency and potentially shorten the duration of CFEs by making foraging riskier and less predictable. Our findings also indicate that, especially in vegetable fields (Fig. 9), the active presence of farmers can deter macaques from entering. Strategies such as avoiding predictable routines (e.g., By varying the timing of field visits randomly instead of adhering to fixed schedules) could further enhance deterrence by increasing the macaques' uncertainty and perceived risk. Long-term strategies, such as sterilization campaigns (Deleuze et al., 2021) directly target group size and could contribute to reducing the extent of CFEs over time. However, such approaches require significant time to achieve effectiveness and are often costly. Alternatively, a strategy more suited to the context of Mauritius could involve widespread trapping efforts. However, similar initiatives in other regions have demonstrated limited success. For example, in Barbados, where vervet monkeys were introduced, a 14-year trapping and export program had little impact on reducing crop foraging (Boulton et al., 1996).

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Lastly, our findings suggest that key CFE parameters can serve as measurable indicators for assessing the effectiveness of deterrents as part of post-intervention monitoring and evaluation (Wallace & Hill, 2012). A successful deterrent would be reflected in reductions in visit frequency, feeding group size, or CFE duration, all of which contribute to minimizing crop losses.

What are farmers' perceptions and attitudes toward macaques, and how are these shaped by socio-cultural factors?

Our findings related to the questionnaire survey highlighted three main axes for discussion: the overall negative perception of farmers toward macaques in Mauritius, the relative increase in crop feeding and negative interactions between people and monkeys since the last few years and lastly, the relative importance of socio-cultural factors.

Overall perception and attitudes. In line with similar studies highlighting the negative perceptions toward non-human primates causing damage to crops (Dore, 2017; Hill & Webber, 2010; Hockings & McLennan, 2016; Mishra et al., 2020), our study found that farmers in Mauritius generally held negative views of macaques. However, these perceptions cannot be fully understood without considering the historical, cultural, and economic contexts in which they arise (Dickman, 2010; Hill, 2004).

For over a century, Mauritius' plantation-based economy, primarily driven by sugar cane cultivation, significantly shaped the island's agricultural landscape. From the 1870s, large sugar estates began selling less productive land to smallholders, influenced by labor shortages and declining sugar prices due to competition from European sugar beet production (Norder et al., 2017). This shift led to historical inequalities in land distribution and reinforced a reliance on monoculture farming, which likely heightened farmers' sensitivity to crop losses, making macaque-induced damage especially detrimental. On the island of St Kitts Green, Dore (2017) highlighted how this transition in the sugar industry altered human-green monkey (*Chlorocebus sabeus*) interactions, as the shift from large-scale to small-scale farming increased contact between farmers and monkeys. Concurrently, agriculture has diversified, shifting away from sugar cane towards crops such as fruits and vegetables—foods that macaques are known to prefer (Sussman & Tattersall, 1986). In a similar context, Horrocks & Baulu (1994) reported that in Barbados, a transition from sugar cane to fruit and vegetable

farming exacerbated human-vervet monkey conflicts. In Mauritius, this agriculture diversification has also led to further encroachment into natural forest areas (Nigel et al., 2015), amplifying the frequency of interactions between farmers and monkeys.

Today, the new fields allocated to farmers are leased from the government, which oversees the allocation process. This creates a situation where farmers have limited control over their environment. Fields at the forest edge are more vulnerable to macaque-induced damage (Lamichhane et al., 2018; Naughton-Treves et al., 1998), while those located centrally or farther from the forest are less affected. This may contribute to a sense of injustice in people, which may further reinforce negative perceptions toward the animals (Dickman, 2010). Additionally, farmers are often unwilling to invest in deterrent methods if they do not own the land (Dore, 2017), explaining the absence of effective deterrents or the reliance on short-term solutions, such as firecrackers.

Contradictions. Another interesting point our study revealed is the discrepancy between the negative perception and the positive self-reported behaviors toward macaques. This inconsistency may stem from social desirability bias, where individuals adjust their responses to align with socially or culturally accepted norms rather than providing an accurate reflection of their true actions or emotions (Grimm, 2010). For example, farmers might state that they avoid hunting macaques to adhere to societal expectations, even if their private attitudes or actual practices suggest otherwise. To mitigate this bias in qualitative research, employing indirect questioning techniques and triangulating data sources is necessary (Carter et al., 2014; Hoffmann & Musch, 2016). Cultural and religious factors, especially among Hindu respondents, could offer another explanation for the discrepancy. While religious beliefs might discourage harmful actions, the frustrations associated with crop losses likely contribute to the negative perceptions (Loudon et al., 2006), creating an internal conflict. Lastly, the willingness to tolerate minor crop loss may be a pragmatic decision rather than a sign of positive perception. Some farmers might see small losses as a manageable compromise, preferring to tolerate damage rather than invest time and resources into preventing all damage or escalating conflicts (Naughton-Treves & Treves, 2005).

Relative importance of socio-cultural factors: As hypothesized, Hindus respondents displayed greater tolerance toward macaques than followers of other religions, likely due to the sacred status of monkeys in Hinduism, where they are associated with the god Hanuman (Knight, 1999; Loudon et al., 2006). Our study confirmed that in Mauritius, Hindus people

were more likely to perceive macaques as sacred compared to those identifying as Muslims or Christians. Interestingly, older farmers (> 41 years old) were less likely to hold this perception of macaque sacredness. Our results may reflect the influence of personal experience. With greater exposure to the challenges posed by macaques, older farmers are likely to show reduced tolerance as they progress through different life stages. This idea is supported by the fact that older farmers were also more likely to support the installation of macaque traps around their plantations. Older farmers may prioritize practical solutions to mitigate crop damage rather than adhering to cultural or religious beliefs. Although it has been suggested that younger individuals tend to hold more positive views on conservation and nature, likely due to higher environmental awareness and risk tolerance (Diamantopoulos et al., 2003; Mazumder et al., 2023), our study did not find greater tolerance among younger farmers as initially hypothesized. This discrepancy may be attributed to the status of *M. fascicularis* in Mauritius, where the species is considered invasive and an agricultural pest (Bertram & Ginsberg, 1994; Sussman et al., 2011). However, we found that farmers with lower educational levels were less likely to view macaques as beneficial. Several studies have already highlighted the influence of educational background on attitudes toward nature and the environment, with less-educated individuals often perceiving nature more negatively (Bhandari & Heshmati, 2010; Hanson et al., 2019).

In a multicultural society like Mauritius, poorly designed interventions risk exacerbating tensions between religious or social groups (Dickman, 2010). For example, trapping is a divisive issue within Mauritian society, particularly within the religious community (Hindu vs. non-Hindu) (Poisson, 2024). These results could be valuable in developing effective public measures and determining the best approach to addressing Mauritius's human-macaque conflict by considering the perspectives of those affected by macaques.

V. CONCLUSION

This study provides valuable insights into the intricate dynamics of human-macaque interactions in the context of crop foraging in Mauritius. By employing a multidisciplinary approach that integrates animal behavior data with human perspectives, we examined the spatial, temporal, and demographic factors driving macaque crop feeding and their associated agricultural impacts on Mauritians. However, we recommend increasing field replication in future studies to account for confounding spatial factors. Additionally, while camera traps

proved useful in identifying patterns of CFEs and large social groups, they are less effective at detecting solitary individuals (Burton et al., 2015; Zak & Riley, 2017), which may have led to an underreporting of individual feeding behavior in our study. Future research should consider increasing the density of camera traps and complementing this remote technique with direct observations to achieve a more nuanced understanding of macaque behavior and their feeding strategies.

Despite these limitations, we demonstrated the influence of demographic, temporal, and spatial factors on crop foraging, with group composition emerging as a key driver of event frequency and duration. CFE frequency was the strongest predictor of crop damage, though all parameters play a critical role. This highlights the need for mitigation strategies that not only reduce CFEs but also address interconnected factors like group size and feeding duration through a holistic approach. Additionally, quantifying CFE parameters can serve as measurable benchmarks to evaluate the effectiveness of deterrence techniques. Our questionnaire data showed that Mauritian farmers share negative perceptions of macaques, shaped by socio-cultural factors (i.e., Religion, age, and education level) establishing a baseline for further research and potentially informing management decision. Successful mitigation requires farmers' active participation, as they are both directly impacted and the most essential actors for designing effective, context-specific solutions (Abondano et al., 2023; Baldauf, 2020).

The macaque situation in Mauritius, though complex, is shaped by ecological, economic and social factors. Given the growing importance of the monkey trade in Mauritius, mostly for biomedical research (Chowdhury, 2024; Hansen et al., 2022), complete eradication of the species from the island would be unlikely due to its high cost and various conflict of interests. Rather than aiming for eradication, we advocate for an informed population control plan based on systematic demographic data of this species in Mauritius. This approach could help provide a sustainable and pragmatic solution that balances ecological, economic, and ethical concerns, enabling responsible management and fostering long-term coexistence.

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APPENDICES

Appendix 1. Questionnaire : Human-Macaque interactions in Mauritius

QUESTIONNAIRE SURVEY (ENGLISH): HUMAN- MACAQUE INTERACTIONS IN MAURITIUS

Research project: Long-tailed Macaques and Humans: assessing perceptions and attitudes of farmers towards macaques.

Target population: The respondents will be selected based on their probability to be concerned by the presence of macaques, assessed by their geographical proximity with the macaque location ("Do you work/live nearby?"). Decision of administration will depend on the answers to questions Q6: no administration if the respondent does not live or work close to the macaque location.

Question 25 until 35 will not be asked to participants if answer to Q10 does not include monkeys.

Respondents should include diverse age cohorts (at least 18 years old) of males and females.

Notes for interviewers:

- If negative answer for the questions Q6: do not pursue the questionnaire.
- Do interview only one planteur per plantation (and not always the man).
- Do record the start time and the end time.
- Most of the questions include the "I don't know" and "no opinion" categories.

Short introduction to be read when approaching randomly chosen respondents:

Hello. I'm a student researcher from the University of Liege (Belgium) I'm studying monkeys in Mauritius and their interactions with humans. I would like to ask you some questions about the monkeys living around. Participation is voluntary and the information collected will be anonymized. We are committed to keeping your answers confidential. The survey will last for approximately 15 minutes. Are you willing to participate? Please note that your participation is completely voluntary, and you can stop the interview at any time.

Provide the informed consent to the respondent.

Preliminary information:

Note for the INT: this data has to be recorded just before the administration of the questionnaire and based on the observation.

Qcontrol1	N°	
Qcontrol2	Date (dd/mm/yy)	
Qcontrol3	Starting time	
Qcontrol4	Location (name)	
Qcontrol5	GPS coordinates	

Hello,

I'm a student researcher from the University of Liege (Belgium) I'm studying monkeys in Mauritius and their interactions with humans. I would like to ask you some questions about the monkeys living around. Participation is voluntary and the information collected will be anonymized. We are committed to keeping your answers confidential. The survey will last for approximately 15 minutes. Are you willing to participate?

Please note that your participation is completely voluntary, and you can stop the interview at any time.

PART A. INFORMATION ON RESPONDENTS

Q1. GENDER	1. M 2. F
Q2. AGE How old are you? (tick one)	1. 18-20 2. 21-30 3. 31-40 4. 41-50 5. 51-60 6. 61 + 999. Refusal
Q3. OCCUPATION What is your profession? (tick one)	1. farmer 2. laborer/worker 3. priest 4. vendor 5. teacher 6. other (specify): 999. Refusal
Q4. EDUCATION LEVEL What is your highest level of education? (tick one)	1. none 2. Primary 3. Secondary 4. Université 7. other (specify): 999. Refusal
Q5. RELIGION What is your religious affiliation? (tick one)	1. Hindu 2. Muslim 3. Christian 4. Buddhist 5. Other 999. Refusal

PART B. PLANTATION INFORMATIONS

Q6. Do you work or live nearby ?	1. Yes 2. No
Q7. What kind of crop do you cultivate ? (tick one or more)	
Q8. What is the size of the plantation: (specify)	
Q9. How long have you had these plantations (specify)	

PART C. PERCEPTIONS AND ATTITUDES

I. PERCEPTIONS

	What kinds of animals, if any, raid your plantation? <i>(tick one or more)</i>	<ol style="list-style-type: none"> 1. Monkeys 2. Rodents 3. Wild pigs 4. Bats 5. Birds 6. Stray dogs 7. Other (specify) :.....
Q11	Which animal causes the most damage? <i>(specify by order of severity)</i>	<ol style="list-style-type: none"> 1. 2. 3. 4. 5. 6.
Q12	Do the macaques negatively impact your livelihood ? <i>(read out tick one)</i>	<ol style="list-style-type: none"> 1. Not at all 2. A little 3. Moderately 4. Very 9. I don't know
Q13	Over these last 30 years, does the macaques' behavior towards people: ? <i>(tick one)</i>	<ol style="list-style-type: none"> 1. has not changed 2. has become less aggressive 3. has become more aggressive 9. I don't know
Q14	Over these last 30 years, does the villager's behavior towards macaques: ? <i>(tick one)</i>	<ol style="list-style-type: none"> 1. has not changed 2. has become less aggressive 3. has become more aggressive 9. I don't know
Q15	What do you feel toward macaques ? <i>(read out and tick one)</i>	<ol style="list-style-type: none"> 1. Happiness 2. Excitement 3. Anger 4. Fear 5. Indifference 7. Other.....
Q16	Have you or a member of your family ever have a physical contact with monkey ? If the answer is yes, please specify how many times and what happened :	<ol style="list-style-type: none"> 1. Yes 2. No 9. I don't know
Q17	Do you consider the macaques sacred? <i>(read out and tick one)</i>	<ol style="list-style-type: none"> 1. Non 2. Yes, a little 3. Yes, very 99. No opinion
Q18	Do you think people consider the macaques less or more sacred than 30 years ago? <i>(read out tick one)</i>	<ol style="list-style-type: none"> 1. Less sacred 2. More sacred 3. Not changed 9. I don't know
Q19	Do you find any benefits in having macaques around? <i>(tick one or more)</i>	<ol style="list-style-type: none"> 1. None advantage 2. Attract revenue to community through tourism 3. Cultural and spiritual value

		4. Educational and recreational value 5. Aesthetic value 6. Ecological value 7. Other (specify): 99. No opinion
Q20	Do you think macaques should be removed from Mauritius ? (<i>read out tick one</i>)	1. Yes, completely removed 2. Yes, but only in certain areas 3. No they shouldn't be removed 99. No opinion
Q21	Do you think macaques are dangerous for human safety? (<i>read out tick one</i>)	1. Yes 2. No 9. I don't know
Q22	Do you think macaques are dangerous for human health?	1. Yes 2. No 9. I don't know
Q23	Do you think macaques can transmit diseases to humans? If yes, which disease do you think macaques can transmit to humans?	1. Yes 2. No 9. I don't know
Q24	Do you think humans can transmit diseases to macaques? If yes, which disease do you think humans can transmit to macaques?	1. Yes 2. No 9. I don't know
Q25	Are the monkeys in groups or alone when you see them?	1. Alone 2. In group 3. It depends 4. Mo pas koné
Q26	If they are in group, approximately how many monkeys come into your plantation? (<i>tick one</i>)	1. < 5 2. 5-15 3. 15-20 4. 20-30 5. 30 or more
Q27	How long have they been raiding your plantation? (<i>tick one</i>)	1. Since always 2. For a few years 3. For a few months 4. Recently started 5. I don't know
Q28	At what time of the day do they come the most?	1. Early morning (before 8am) 2. Late morning (8 AM - 12 PM) 3. Afternoon (12 PM - 4 PM) 4. Evening (4 PM - 8 PM) 5. Night (after 8 PM) 6. Any time if no one in the field 6. I don't know / it varies

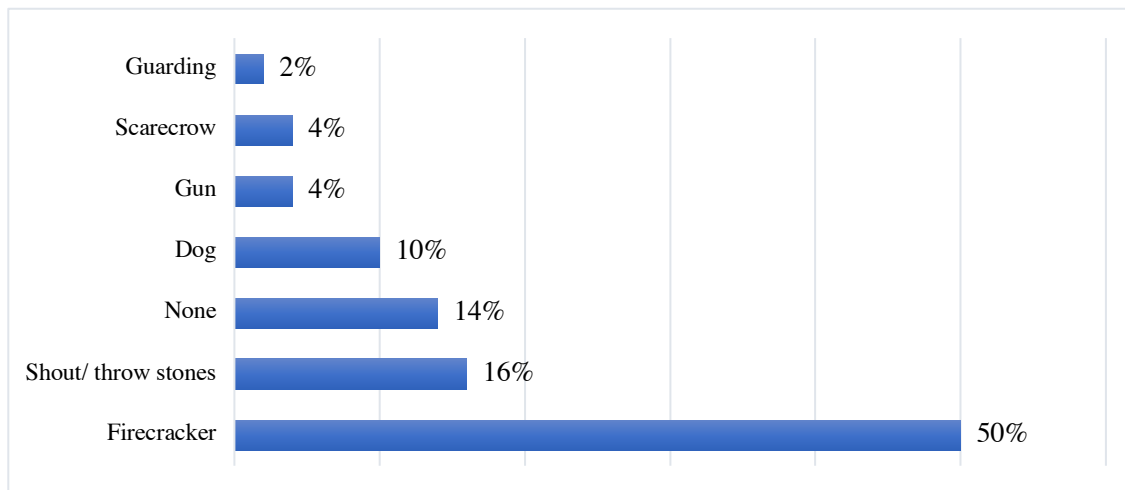
II. SELF-REPORTED BEHAVIORS AND NUISANCES

	How much do you estimate you have lost because of the monkeys? (%)	1. Less than 10% 2. 20-40% 3. 50-70% 4. More than 70% 5. Anything 9. I don't know
Q30	How often do macaques enter your plantation ? <i>(tick one)</i>	1. never 2. Less than once a month 3. At least once a week 4. Every day 9. I don't know
Q31	What do you do when you see macaques in your plantation? <i>(tick one)</i>	1. crying out/ making noise 2. chase/lunge 3. throwing stones 4. throwing branches 5. firework 6. gun 7. physical aggression 8. Poison 9. none 999. Refusal
Q32	Is it effective ?	1. Yes, completely 2. Yes a little 3. Not at all
Q33	What kind of your crops do the macaques raid the most? <i>(tick one or more)</i>	1. Carrots 2. Chouchou 3. Aubergines 4. Sugar canes 5. Manioc 6. Potatoes 8. Everything 9. Other : 9. I don't know
Q34	Have you ever considered or already adapted your crops because of monkeys?	1.Yes 2.No 99. No opinion
Q35	Have you ever plan or adapted to move because of macaques ?	1.Yes 2.No 99. No opinion
Q36	Over the last 10 years, has the macaques' frequency of crop raiding: ? <i>(read out and tick one)</i>	1. increased 2. decreased 3. not changed 9. I don't know
Q37	How do you feel about macaques taking a portion of your harvest ?	1. I agree 2. I don't agree 3. I don't know
Q38	Which ones of the following behaviours did macaques already have towards you or a member of your family ? : <i>(read out and tick one or more)</i>	1. threat/intimidation 2. lunch/chase 3. slap 4. scratch 5. bite 6. other <i>(specify):.....</i> 9. I don't know
Q39	Did you already eat macaques? <i>(tick one)</i>	1. yes 2. no 999. Refusal
Q40	Do you hunt macaques? <i>(tick one)</i>	1. yes 2. no 999. Refusal
Q41	Do you have traps around your plantation?	1. yes

		2. no 9. I don't know
Q42	Do you find them effective in reducing the amount of damage to crops?	1. yes, definitely 2. yes but moderately 2. no, not at all 9. I don't know
Q43	Would you support an increase in trapping efforts around your plantation?	1. yes, definitely 2. yes but with certain conditions 2. no, not at all 9. I don't know
Q44	What kind of solutions would you put in place to manage the problems with the macaques?	Specify: 9. I don't know 99. I have no interest in finding a solution
Q45	Would you like to discuss about something else ?	Specify:

Qcontrol6	End time	
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Appendix 2. Deterrent methods employed by all respondents that answered to the question “How do you repel macaques” (n = 55).



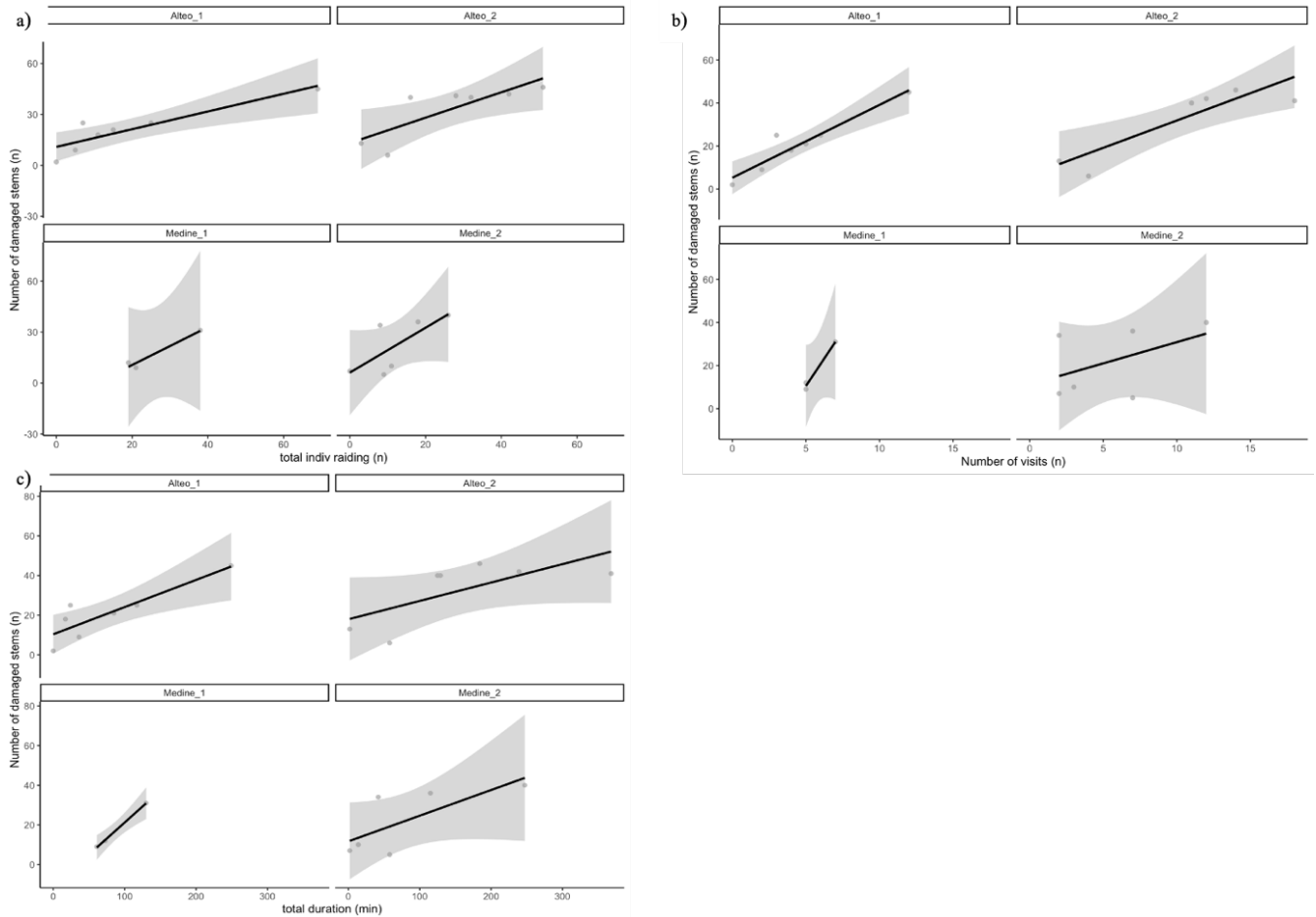
Annexe 3. Output of logistic regression models for 5 item questions with 3 predictors (age, religion, education level). Only significant ($p < 0.05$) and marginally significant ($p < 0.07$) values are presented.

Predictors	Category	Response variables	Estimate	SE	z	p-value
<i>Religion</i>	Hindus	-	-	-	-	-
	Other religions	Sacred	-1.3949	0.687	-2.029	<0.05
		Elimination	-1.14316	0.676	-1.691	0.07
<i>Age</i>	Old	Sacred	-0.9604	0.631	-1.524	0.07
		More capture	1.7430	0.832	2.093	<0.05
	Young	Macaque presence	-2.3235	-1.006	-2.309	<0.05
<i>Education Level</i>	Low	Macaque presence	-1.65596	0.829	-1.996	<0.05
	High	-	-	-	-	-

Appendix. 4. Total number of fortnights monitored, total number of CFE parameters recorded for each site throughout the entire study period and standardized CFE rates as the number of CFEs per fortnight

Sites	Type of crop	Number of fortnights	Total number of CFEs	CFE rate per fortnights
Alteo 1	Sugar cane	7	32	5.33 (± 3.56)
Alteo 2	Sugar cane	7	72	10.29 (± 5.56)
Medine 1	Sugar cane	3	17	5.67 (± 1.15)
Medine 2	Sugar cane	6	33	5.50 (± 3.94)
Bellevue 5	Eggplant	5	19	3.80 (± 1.30)
Plainsophie 6	Chouchou	6	20	3.33 (± 2.42)

Appendix 5. Relationship between key CFE paramaters (i.e., Number of visits, total feeding individuals, and total duration) and the number of damaged sugarcane stems (n). Each plot represents a different predictor: (a) Total individuals feeding (n), (b) Number of visits (n) Total individuals feeding (n), and (c) Total duration (min). Points represent individual observations, and the black line shows the fitted linear regression. Error bars in grey indicate the confidence intervals for the regression.



Appendix 6. Spatial characteristics for each study sites with the proportion of forest, the roportion of farmland and distance to building (meters).

Site	Proportion of forest	Proportion of farmland	Distance to buildings (m)
Alteo 1	0,22	0,606	812,37
Alteo 2	0,377	0,606	1708,11
Medine 1	0,175	0,411	357,06
Medine 2	0,388	0,323	1297,96
Bellevue	0,225	0,417	82,34
Plaine Sophie	0,604	0,28	176,91

Appendix 7. List and relative abundance of tree species (DBH > 5 cm) identified along the phenological transects in each study site with the fruit type (i.e., fleshy/non-fleshy) and the geographic origin (i.e., Native/Non-native)

Species	Fruit type	Geographic origin
Alteo 1		
<i>Ardisia elliptica</i>	Fleshy	Non-native
<i>Erythrospermum monticolum</i>	Non-fleshy	Native
<i>Ficus reflexa</i>	Fleshy	Native
<i>Grangeria borbonica</i>	Fleshy	Native
<i>Harunga madagascariensis</i>	Fleshy	Native
<i>Ligustrum robustum</i>	Fleshy	Non-native
<i>Litsea glutinosa</i>	Fleshy	Non-native
<i>Litsea monopetala</i>	Fleshy	Non-native
<i>Mikania micrantha</i>	Non-fleshy	Non-native
<i>Nuxia verticillata</i>	Non-fleshy	Native
<i>Psidium cattleianum</i> Sabine	Fleshy	Non-native
<i>Ravenala madagascariensis</i>	Fleshy	Non-native
<i>Syzygium jambos</i>	Fleshy	Non-native
Total no. of stem = 325 No. of species = 13		
Alteo 2		
<i>Camellia sinensis</i>	Non-fleshy	Non-native
<i>Ligustrum robustum</i>	Fleshy	Non-native
<i>Litsea monopetala</i>	Fleshy	Non-native
<i>Mikania micrantha</i>	Non-fleshy	Non-native
<i>Pandanus</i> sp.	Non-fleshy	Non-native
<i>Psidium cattleianum</i> Sabine	Fleshy	Non-native
<i>Ravenala madagascariensis</i>	Fleshy	Non-native
<i>Syzygium jambos</i>	Fleshy	Non-native
<i>Tisonia costata</i>		Non-native
Total no. of stem = 239 No. of species = 9		
Medine 1		
<i>Cissus rotundifolia</i>	Fleshy	Native
<i>Eucalyptus tereticornis</i>	Non-fleshy	Non-native
<i>Haematoxylum campechianum</i>	Non-fleshy	Non-native
<i>Hiptage benghalensis</i>	Non-fleshy	Non-native
<i>Leucaena leucocephala</i>	Non-fleshy	Non-native
<i>Litsea glutinosa</i>	Fleshy	Non-native
<i>Melia azedarach</i>	Fleshy	Non-native
<i>Mikania micrantha</i>	Non-fleshy	Non-native
<i>Murraya paniculata</i>	Fleshy	Non-native
<i>Operculina turpethum</i>	Non-fleshy	Native
<i>Paederia foetida</i>	Non-fleshy	Non-native
<i>Pongamia pinnata</i>	Non-fleshy	Non-native

<i>Schinus terebinthifolia</i>	Fleshy	Non-native
<i>Tabebuia rosea</i>	Non-fleshy	Non-native
<i>Terminalia arjuna</i>	Non-fleshy	Non-native
<i>Vachellia nilotica</i>	Non-fleshy	Non-native

Total no. of stem = 262

No. of species = 16

Medine 2		
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<i>Adenanthera pavonina</i>	Non-fleshy	Non-native
<i>Albizia lebbek</i>	Non-fleshy	Non-native
<i>Cordia myxa</i>	Fleshy	Non-native
<i>Dimocarpus longan</i>	Fleshy	Non-native
<i>Doratoxylon apetalum</i>	Fleshy	Native
<i>Elaeodendron orientale</i>	Fleshy	Native
<i>Eugenia uniflora</i>	Fleshy	Non-native
<i>Haematoxylum campechianum</i>	Non-fleshy	Non-native
<i>Hiptage benghalensis</i>	Non-fleshy	Non-native
<i>Ipomoea corymbosa</i>	Non-fleshy	Non-native
<i>Litsea glutinosa</i>	Fleshy	Non-native
<i>Mangifera indica</i>	Fleshy	Non-native
<i>Melia azedarach</i>	Fleshy	Non-native
<i>Morinda citrifolia</i>	Fleshy	Non-native
<i>Murraya paniculata</i>	Fleshy	Non-native
<i>Persia americana</i>	Fleshy	Non-native
<i>Schinus terebinthifolia</i>	Fleshy	Non-native
<i>Senegalia rugata</i>	Non-fleshy	Non-native
<i>Syzygium cumini</i>	Fleshy	Non-native
<i>Tabebuia pallida</i>	Non-fleshy	Non-native
<i>Tamarindus indica</i>	Fleshy	Non-native
<i>Terminalia arjuna</i>	Non-fleshy	Non-native
<i>Vachellia nilotica</i>	Non-fleshy	Non-native

Total no. of stem = 208

No. of species = 23

Plaine Sophie		
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<i>Camphora officinarum</i>	Fleshy	Non-native
<i>Camellia sinensis</i>	Non-fleshy	Non-native
<i>Hiptage benghalensis</i>	Non-fleshy	Non-native
<i>Ligustrum robustum</i>	Fleshy	Non-native
<i>Litsea glutinosa</i>	Fleshy	Non-native
<i>Litsea monopetala</i>	Fleshy	Non-native
<i>Mussaenda arcuata</i>	Fleshy	Native
<i>Pinus elliottii</i>	Non-fleshy	Non-native
<i>Psidium cattleianum Sabine</i>	Fleshy	Non-native
<i>Ravenala madagascariensis</i>	Non-fleshy	Non-native
<i>Vachellia nilotica</i>	Non-fleshy	Non-native

Total no. of stem = 412

No. of species = 11

Bellevue		
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<i>Adenanthera pavonina</i>	Non-fleshy	Non-native
<i>Albizia lebbek</i>	Non-fleshy	Non-native
<i>Ardisia elliptica</i>	Fleshy	Non-native
<i>Musa sapientum</i>	Fleshy	Non-native
<i>Carica papaya</i>	Fleshy	Non-native
<i>Cissus rotundifolia</i>	Fleshy	Native
<i>Dimocarpus longan</i>	Fleshy	Non-native
<i>Doratoxylon apetalum</i>	Fleshy	Native
<i>Eugenia uniflora</i>	Fleshy	Non-native
<i>Ficus reflexa</i>	Fleshy	Native
<i>Flacourtia indica</i>	Fleshy	Non-native
<i>Haematoxylum campechianum</i>	Non-fleshy	Non-native
<i>Hiptage benghalensis</i>	Non-fleshy	Non-native
<i>Ipomoea sp.</i>	Non-fleshy	Non-native
<i>Leucaena leucocephala</i>	Non-fleshy	Non-native
<i>Litsea glutinosa</i>	Fleshy	Non-native
<i>Litsea monopetala</i>	Fleshy	Non-native
<i>Mangifera indica</i>	Fleshy	Non-native
<i>Melia azedarach</i>	Fleshy	Non-native
<i>Mikania micrantha</i>	Non-fleshy	Non-native
<i>Operculina turpethum</i>	Non-fleshy	Native
<i>Pongamia pinnata</i>	Non-fleshy	Non-native
<i>Premna serratifolia</i>	Fleshy	Native
<i>Psidium cattleianum</i>	Fleshy	Non-native
<i>Santalum album</i>	Fleshy	Non-native
<i>Schinus terebinthifolia</i>	Fleshy	Non-native
<i>Scutia myrtina</i>	Fleshy	Native
<i>Senegalia rugata</i>	Non-fleshy	Non-native
<i>Syzygium cumini</i>	Fleshy	Non-native
<i>Syzygium jambos</i>	Fleshy	Non-native
<i>Tabebuia rosea</i>	Non-fleshy	Non-native
<i>Terminala catappa</i>	Fleshy	Non-native
<i>Ipomoea indica</i>	Non-fleshy	Non-native
Total no. of stem = 352		
No. of species = 33		

Appendix 8. a) Field control with absence of crop feeding evidence (i.e., sugarcane peelings and no visible damage to the field edge). b) Field showing evidence of macaque crop feeding, including sugarcane peelings and visible damage to the field edge c) Impact of repeated macaque feeding over the years: the first rows of sugarcane are gradually eaten away, preventing regrowth and causing the field edge to recede.



Appendix 9. Camera trap positionned in the field with a coated flexible wire and a padlock.



Appendix 10. Fortnight, weekly and absolute frequency of CFEs and average damages in sugarcane and vegetable fields with standard error

<i>Sites</i>	<i>Number of damages</i>	<i>CFEs rate per fortnights</i>	<i>CFEs rate per weeks</i>	<i>CFEs relative frequency¹</i>
Alteo 1	20.7 ± 13.7	5.33 ± 3.56	3.56 ± 2.01	0.30
Alteo 2	32.6 ± 16.00	10.29 ± 5.56	5.54 ± 2.82	0.67
Medine 1	17.3 ± 11.90	5.67 ± 1.15	5.67 ± 1.15	0.37
Medine 2	22 ± 16.30	5.50 ± 3.94	3.0 ± 2.94	0.34
Bellevue	217.8 ± 83.58	3.80 ± 1.30	1.09 ± 0.99	0.23
Plaine Sophie	5.5 ± 5.17	3.33 ± 2.42	2.13 ± 1.25	0.32