

The effects of fruit availability on diet composition and feeding behaviour of invasive *Macaca fascicularis* in Mauritius: implications for conservation of *Pteropus niger* and native forests

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Note to the reader

The main focus of this report is the tracking study that was carried out in Mauritius from December 2019 until February 2020. The introduction and discussion focus solely on this study. However, as part of the Rufford grant, we have initiated a study on the effects of plant invasion on fruit production of native trees in October 2019. To provide an update on this ongoing project, we have added a method section and a small result section that have been separated from the main body of text (Ecology of *M. fascicularis*) with a different subheading (Weeding experiment).

Introduction

Macaca spp. are opportunistic omnivores that mainly include fleshy fruits in their diet (Lucas and Corlett, 1991; O'Brien and Kinnaird, 1997; Albert et al., 2013; Sengupta and Radhakrishna, 2016; Gazagne et al., 2018), generally prefer ripe over unripe fruit (Sengupta and Radhakrishna 2015; Ruslin et al., 2019) and can be important seed dispersers (Albert et al., 2013a), especially in areas where other large seed-dispersers have disappeared (Lucas and Corlett, 1998; Sengupta et al., 2014). Furthermore, *Macaca* spp. are known to feed on leaves, flowers, immature fruits, and seeds in times of fruit scarcity, just like other frugivorous primates (Terborgh 1983; Wallace 2005). Macaques are known to increase the proportion of these plant items in their diet during periods of fruit shortage (Lucas and Corlett, 1991; Yeager et al., 1996; Sengupta and Radhakrishna, 2016; Tang et al., 2016) and thus these food items are typically referred to as 'fallback foods' (Marshall et al., 2009). Moreover, in places where fruits are generally scarce, the diet of *Macaca* spp. can even be predominantly folivorous (Hanya, 2004; Huang et al., 2015; Tang et al., 2016). This is well illustrated by both *Macaca assamensis* and *Macaca mulatta*, which are highly folivorous in limestone forests and are known to shift to a more frugivorous diet in periods of high fruit abundance (Huang et al., 2015; Tang et al., 2016). The majority of fruits in their diet are then typically consumed at an immature stage (Huang et al., 2015; Tang et al., 2016). As a consequence, seed-dispersal effectiveness by *Macaca* spp. may be dictated by (both year-round and seasonal) fruit scarcity, since a shift from a highly frugivorous diet to a diet that mainly consists of "fallback foods" (leaves, stems, immature fruits, seeds, flowers) would mainly lead to destruction of seeds.

Ranging patterns of *Macaca* spp. are also typically driven by fruit availability (Albert et al., 2013b; Sengupta and Radhakrishna, 2016; Gazagne et al., 2018). *Macaca* spp. commonly adopt both energy maximizing and minimizing strategies in periods of fruit scarcity (Agetsuma and Noma, 1995; Albert et al., 2013b). Energy-maximizing strategies involve increasing ranging distance during periods of fruit scarcity to meet dietary needs and obtain sufficient nutrients (Hall, 1962). On the other hand, energy-minimizing strategies involve decreasing daily travel distances and increasingly foraging on lesser quality ("fallback foods") food items (Wrangham, 1977). These patterns often differ between disturbed habitat (e.g. settlements, degraded forests and agricultural areas) and undisturbed habitat (Sussman et al., 2011; Albert et al., 2013b; Mohammad and Wong, 2019). In undisturbed habitat, macaques have smaller home ranges with shorter day ranges and generally spend less time travelling and foraging and more time resting (Altmann and Muruthi, 1988; Kogenezawa and Imaki, 1999; Saj et al., 1999) compared to macaques in fragmented and disturbed habitat (Sha and Hanya, 2013). Moreover, less wild fruits and more anthropogenic food sources are typically included in the macaque's diet in disturbed habitat, which is potentially further promoted by lower overall fruit availability compared to undisturbed habitat (Sha and Hanya, 2013).

The long-tailed macaque, *Macaca fascicularis*, is a macaque species native to most of Southeast Asia and occurs in a broad variety of habitats (Aldrich-Blake, 1980; Gumert, 2011). Like other macaques, this species is a highly opportunistic omnivore (Gumert, 2011), prefers feeding on fleshy fruits (Lucas and Corlett, 1991; Ruslin et al., 2019) and can be an effective

seed disperser (Lucas and Corlett, 1998). However, it has been both deliberately and accidentally introduced to oceanic islands across the globe, where it has severe ecological impacts (GISD, 2019). *Macaca fascicularis* adapts remarkably well to habitat disturbed by humans (Medway, 1970; Van Schaik et al., 1996; Sussman et al., 2011), which is typically present on islands. Besides exploiting crops (Sussman et al., 2011), they have a number of ecological impacts, including predation of eggs and chicks of native birds, destroying native fruits and seeds and changing the composition of the vegetation (Carter and Bright, 2002; Kemp and Burnett 2003). As a result, *M. fascicularis* is included in the IUCN invasive species specialist group's list for the 100 most invasive species worldwide (GISD, 2019). Introduced non-hominid primates worldwide, including *M. fascicularis*, are either partly or completely accountable for at least 69 island extinctions and extirpations (Jones et al., 2018).

In Mauritius, *M. fascicularis* is highly invasive and known to predate eggs and chicks of endemic birds (Jones et al., 1992; Safford, 1994) and consume and destroy immature fruit (Reinegger et al., 2020 under review), flowers and young shoots of endemic plants (Baider and Florens, 2006). The island was once almost completely covered by forests (Cheke, 1987), but now the majority of land cover is made up of urban areas and agricultural land. Forests cover about 25% of Mauritius (MAIFS, 2015), but only a small portion (1%) is good quality native vegetation that is not dominated by alien invasive plants (forests with >50% native plant cover; MAIFS, 2015). The scarce native fruits that remain in what is left of the native forests are mostly shared between *M. fascicularis*, other invasive animals (e.g. *Rattus rattus* and *Psittacula krameri*) and the endemic flying fox *Pteropus niger*. Additionally, the macaque population has thrived and is likely to have drastically grown in size in the last 20 years (Bertram, 1994). Therefore, native fruit availability may be low, possibly promoting consumption of unripe fruit and seeds by *M. fascicularis* and thus ineffective seed-dispersal. Furthermore, the consumption of immature fruit by *M. fascicularis* may reduce availability of native fruit to the effective seed-disperser *P. niger* that eats mostly ripe fruit (Krivek et al., 2020; Reinegger et al., 2020 under review), potentially disrupting seed dispersal by *P. niger* and affecting forest regeneration.

In the latest study on the population dynamics of *M. fascicularis* in Mauritius (Bertram, 1994), the population was estimated at about 40000 individuals. The author argued that the population could be doubled in 6 years if it was below carrying capacity, because of the lack of natural predators and high birth rate. Native forests are unlikely to sustain a growing population of *M. fascicularis*, since these remnant forests seem to barely provide sufficient resources for *P. niger*. It is likely that *M. fascicularis* has come to rely largely on 'fallback foods' and anthropogenic food sources in Mauritius because of the potentially low native fruit availability in the highly disturbed forest habitat. Previous studies on *M. fascicularis* in Mauritius found that *M. fascicularis* spends a larger proportion of their feeding time consuming leaves, flowers, grass and sugarcane (42%) than fruits (38%) (Sussman et al., 2011). Additionally, *M. fascicularis* spends a significantly higher proportion of time feeding on stems and flowers during the dry season than in the wet season when fruits are expected to be more abundant (Sussman et al., 2011), suggesting seasonal fruit scarcity. However,

seasonal fruit availability has never been measured, and thus there is no robust evidence that fruits are a preferred resource and leaves and flowers act as 'fallback foods'.

Therefore, we aimed to quantify the consumption of native fruits and damage to native plants by *M. fascicularis* in a degraded native forest remnant and study the relationship between seasonal fruit availability, ranging patterns and diet composition of *M. fascicularis*. Furthermore, we aimed to estimate macaque density in order to provide a new population estimate based on a similar approach as described in the population study on *M. fascicularis* in Mauritius by Bertram (1994). Consequently, we hypothesized that *M. fascicularis* spends a larger proportion of feeding time consuming fruits during periods of high fruit availability than in periods of low fruit availability. We also tested the hypothesis that *M. fascicularis* feeds on more unripe fruits during periods of fruit scarcity. Furthermore, because the distribution of forest resources is likely to be patchy, we hypothesized that *M. fascicularis* uses energy-maximizing strategies to acquire preferred food sources during periods of low fruit availability. We then discuss the implications of our findings for the conservation of *P. niger* and native forests.

Methods

Ecology of *M. fascicularis*

Study site

This study was carried out in a forest remnant in the North of Mauritius (Fig. 1), selected for its native plant richness and the presence of *M. fascicularis*. The forest covered two mountains: Calebasses mountain range and Mariannes (lat: -20.181203°, long: 57.584498°). This area was between 420 and 580 m asl and rainfall is 2,500 – 4,500 mm/year. The forest was made up of semi-dry vegetation at lower elevations and sub-humid vegetation at higher elevations. However, the forest was extremely degraded at lower elevations and mostly consists of a remnant pine plantation (*Pinus nigra*) and dense thickets that were made up of invasive *Hiptage benghalensis*, *Ligustrum robustum*, *Litsea* spp., *Psidium cattleianum* and *Syzygium jambos*.

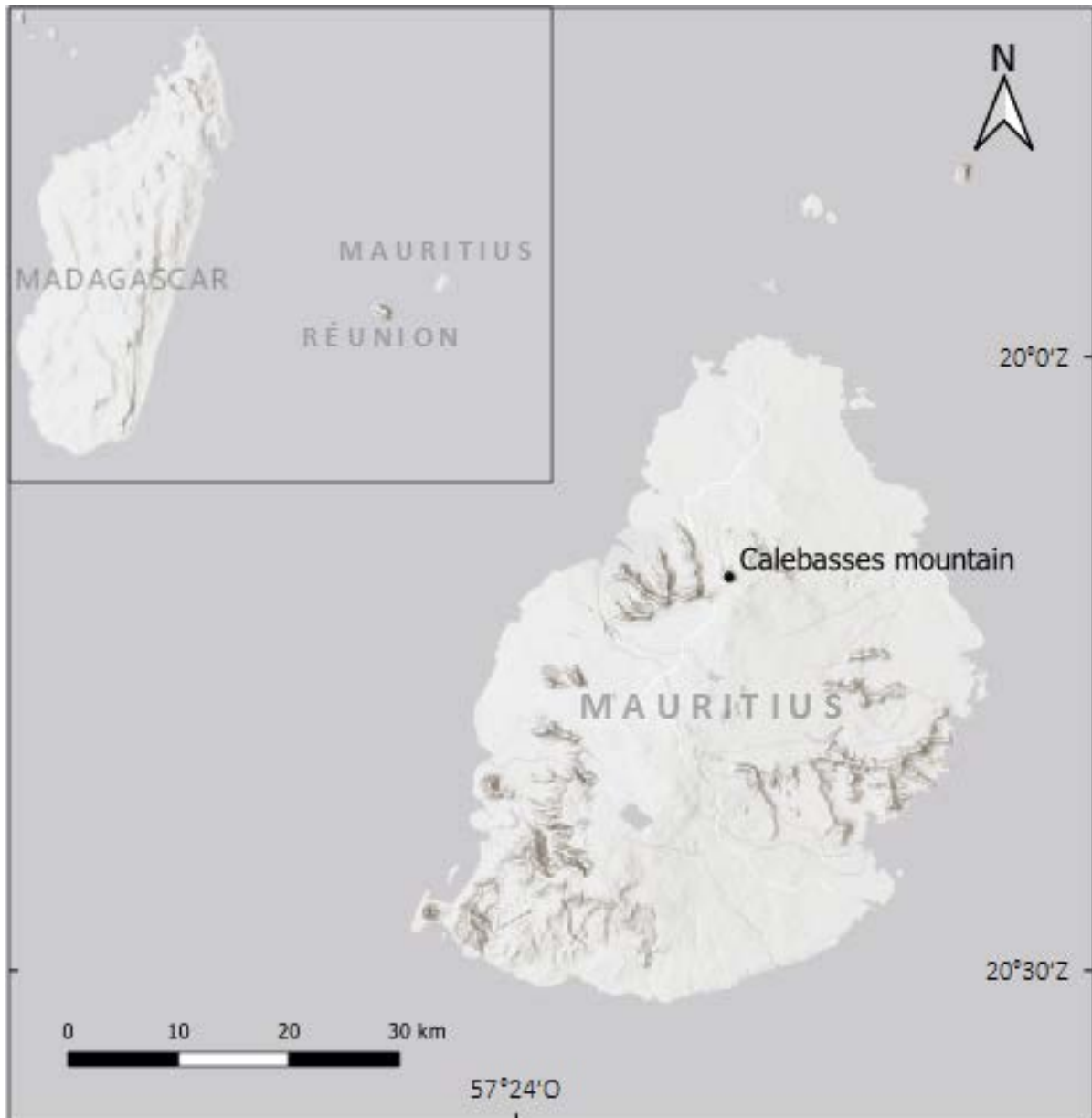


Figure 1: Location of the study site

Behavioural data collection

A troop of macaques occupying the valley connecting Calebasses mountain and Mariannes were habituated during October – November 2019 (Fig. 2). Chasing animals was avoided as much as possible by memorizing areas they frequently visited during the day, so that the animals could run into the researcher instead of vice versa. The troop consisted of 19 – 23 individuals and was followed two to three times a week between December 2019 and February 2020 from the moment the troop left their sleeping site (05:30 – 6:00) until 13:30. This day interval was chosen over full days (06:00 – 18:00) because the high topographical relief in the area combined with steep slopes made following the group very physically straining. Multiple opportunistic observations of the study troop done in the late afternoon during phenology surveys indicated that the troop remained active until around 18:30. However, Sussman et al., (2011) found that activity patterns of Mauritian *M. fascicularis* were

very consistent throughout the day, suggesting that our chosen day interval can be representative for the whole day. Behavioural data was collected by scan sampling the troop at 5-min intervals (Altmann, 1974), typically within five to 20 m distance from the troop. During scans, each visible troop member was observed for 15 - 20 seconds to record its behaviour. Behavioural activities were divided into seven categories: resting, moving, feeding, grooming, playing, mating and fighting. Feeding was defined as the manual handling of food items and then putting them into the mouth or oral handling of food items when they were directly taken by the mouth. When an individual was feeding, the first item that was consumed was noted: pine cone, insect, fruit, leaf, bark, flower or seed (the name of the plant species was recorded for each plant food). For each activity, we also recorded whether it occurred in the canopy or on the ground. Activity patterns were analyzed in R (R Core Team, 2020) by calculating the relative proportion of scans that macaques were engaged in each activity every month. Additionally, diet composition and relative use of plant species were analyzed by calculating the relative proportion of time the macaques spent feeding on every food item and plant species. Moreover, we used Mann-Whitney U - tests to test for differences in daily use of food items between months. January was omitted from these analyses, because frequent cyclones and torrential storms made data collection nearly impossible during this month.



Figure 2: A section of the sleeping site of our study troop located next to a gully in the central valley of Callebasses mountain range (top left). Trees used for sleeping are usually covered by the liana *Hiptage benghalensis*, which makes excellent hammocks (top right and bottom). Macaques can be seen resting in the *H. benghalensis* covered trees.

Quantification of fruit consumption

Fruit damage and consumption was opportunistically quantified while following the troop. The exact time that a macaque or a group of macaques started feeding was recorded and the number of macaques that were involved in this feeding event was noted. Focal sampling of

one randomly selected individual for as long as the feeding event lasted was used to determine the part of the consumed fruit (whole fruit, pulp, seed). The state of ripeness of fruits was also determined (ripe/unripe) and the type of fruit consumption was recorded: swallowed (when the entire fruit was ingested), spat out (when the fruit was taken into the mouth, mostly stored in cheek pouches, cleaned of the pulp and the seeds spat out), partly eaten (when portions of fruits, e.g., epicarp, were fed upon and then discarded), destroyed (when seeds were crunched by macaques) and dropped (when fruits were picked and discarded without being fed upon or accidentally dropped). Breaking of branches by macaques during the feeding session was also recorded. After the macaques finished feeding, the fruits and other plant parts (seeds, flowers, leaves and branches) dropped by macaques were counted beneath the feeding tree for 2 to 3 minutes or collected and stored in zip-lock bags to allow quantification after the end of field activities on the same day. The total number of eaten fruits and other plant parts were then divided by the total number of macaques on the tree to estimate consumption by a single macaque, as distinguishing fruits handled by different individuals on the same tree in dense vegetation was not possible. Furthermore, we could not quantify all the eaten fruits (especially *Flacourtia indica* and *Litsea* spp.) because *M. fascicularis* often stored fruits in its cheekpouches and would continue eating them outside of the feeding tree (Fig. 3). January was included in the analysis, since feeding events from all months were pooled together.



Figure 3: A macaque feeding on pine cone of *Pinus nigra* (left), a macaque plucking leaves of *Ligustrum robustum* (middle) and a macaque chewing on fruits of *Litsea* spp. and *Flacourtia indica* stored in its cheekpouches (right).

Fruit availability and fruit yield

Fruit availability within the home range of our study group was assessed by estimating fruit cover along three transects outside of the remnant pine plantation. Two were oriented in the North–South direction and one was oriented East–West. Each transect was 2 m wide and 200 m to 400 m in length (total length of 900 m). *Macaca fascicularis* is considered an opportunistic feeder in its native home range (Gumert, 2011) as well as in Mauritius (Sussman

et al., 2011) and is expected to feed on any fruit that is available. Therefore, all species present in the phenology transects were included and all trees with diameter at breast height (DBH) ≥ 5 cm and lianas present on the trees were marked along the four transects.. Every month, the phenological state of the trees and the lianas was recorded (presence/absence of young leaves, flowers, ripe and unripe fruit). Based on the percentage of crown area covered by fruit (visual estimation), trees were ranked on a 5-point scale where a score of 0 implied no fruit and 1, 2, 3, and 4 implied 1–25 %, 26–50 %, 51–75 %, and ≥ 76 % of the crown area covered by fruit respectively (Albert et al., 2013b; Sengupta and Radhakrishna, 2016). Fruit Availability Index (FAI) was calculated for each month:

$$FAI = \sum_{i=1}^n D_i B_i P_{im}$$

Here, D_i is the mean density of species i in the home range, B_i is the mean basal area of trees of species i (cm^2) and P_{im} is the mean phenology score of fruit in species i in month m . This is then totalled for all species (n) in the phenology transects. Diet composition and home range were compared between months. However, additional months of data collection are needed so that Spearman's rank correlation coefficients can be calculated to understand the relationship between FAI and diet composition.

Moreover, to provide a measure of fruit yield of trees along our transects, total number of fruit on trees > 4 m tall was estimated in January and February by counting the number of fruits using binoculars along three large branches on a tree that were selected on an *ad libitum* basis. The mean number of fruits per branch was calculated and then multiplied by the number of major branches on the tree. For small trees (≤ 4 m tall) all the fruits were counted. Similar methodologies have been used for estimating fruit abundance of tropical trees in other studies (Dinerstein, 1986; Chapman et al., 1992).

Home range and daily travel

On tracking days, the location of the group was manually recorded with a handheld GPS (Garmin eTrex 30x) every 30 min. An equal number of GPS points was collected for every month ($n = 76$). QGIS and R were used to map the monthly home range and calculate the length of daily paths. Estimates of limits and surfaces of the day range were derived by using the least square cross-validated fixed kernel density estimation (LSCV KDE) in R (script can be found in Appendix 2). This method is one of the most widely used and is an accurate method for home range size estimation (Seaman and Powell 1996; Albert et al., 2013b). The 95% confidence region of the kernel density estimation (95% KDE) was used to represent the full home range and reflects the area associated with a 95% probability of finding the animal. The 50% confidence region (50% KDE) was also calculated, reflecting the core area that is disproportionately more used by the animals than other areas of the home range (Rühhmann et al., 2019). The monthly 95% and 50% KDE's created in R were exported as shapefiles and mapped in QGIS. To test differences in daily path lengths between months, we used Mann-Whitney U - tests. Since the number of recorded GPS points differed between days, daily path length was expressed as path length per 30-min interval (distance between consecutive GPS points per day for every month).

Population estimate

Macaque population can be estimated by extrapolating the macaque density in one area to all forested areas in Mauritius (Bertram, 1994). However, macaque densities vary greatly across the island. For example, degraded open woodland habitat in the Southwest of the island facilitates much bigger macaque numbers compared to forest habitat far away from cultivation and access to human food (1.3 individuals per ha compared to 0.3 individuals per ha, Bertram, 1994). Therefore, we assumed that forest habitat within 1 km from cultivation supports the macaque density found in our study and that areas further than 1 km from cultivation can only support half of this density. The total area of suitable macaque habitat within and outside of 1 km was estimated with vegetation and land cover maps in QGIS.

Weeding experiment

Invasive plant impact on native fruit production

The study was carried out in the forest remnant covering Calebasses mountain (Fig. 1). To assess the impact of invasive plants on fruit production of native plants, the fruit production of canopy species that are primarily dispersed by bats were monitored in pre-weeded conditions and are going to be monitored in post-weeded conditions. Fruit drop of a total of three to four canopy tree replicates was measured in a total of 15 plots (10 m by 10 m). The plots were placed at > 10 m distance away from each other and divided into three treatments: unweeded (five plots), single-weeded (only weeded once) and multi-weeded (weeded every four months). Only canopy species that were sufficiently abundant to be replicable in the study site were selected: *Aphloia theiformis*, *Calophyllum tacamahaca*, *Eugenia pyxidata*, *Labourdonnasia calophylloides*, *Psiloxylon mauritianum*, *Sideroxylon puberulum*, *Syzygium glomeratum* and *Syzygium duponti*. The three to four replicates in every plot were a random subset of these species. The replicates were selected three to five meters away from the edge of the plots, to minimize edge-effects after weeding. Fruit drop was measured with seed traps, constructed of polyester fabric loosely stretched along a square pvc frame (1 m by 1 m). Two frames were placed under the canopy of every replicate and tied at least 0.5 m above the ground at all edges with plastic string to minimize fruit and seed removal by rats (Fig. 4). Fruit production was monitored in unweeded conditions in every plot from October 2019 until the April/May 2020. The seed traps were checked on a weekly basis from the start of the flowering until the end of the fruiting period for each tree. All fruits (intact and eaten), seeds (intact and eaten) and bat ejecta pellets (compressed fibrous material that remains after *P. niger* squeezes the juice from the flesh) were recorded. Fruits eaten by *P. niger* were identified by their typical triangular-shaped canine imprint (Banack 1998; McConkey and Drake 2015; Reinegger et al. 2020 under review). The teeth marks could be easily distinguished from marks left by other common large canopy feeders: the invasive long-tailed macaque (*Macaca fascicularis*) leaves large round canine marks (Krivek, 2017; Reinegger et al., 2020 under review), invasive rats (*Rattus rattus*) leave gnawing marks with their two upper and lower incisors and ringneck parakeets (*Psittacula krameri*) create V-shaped marks with their under and upper mandibles (VSG, 2018). Additionally, a single camera trap was placed on the trunk of one fruiting tree replicate per species and aimed at the canopy. A 10 second video was recorded when motion is detected, and the camera trap was left for two

weeks. This will be repeated for every selected canopy species so that the identity of animals feeding on the species can be confirmed.



Figure 4: Seed traps placed under the canopy of native trees in the study site.

All plots, except for the ones to which the ‘unweeded’ treatment is applied, are going to be weeded when the majority of our selected species stop fruiting (end of fruiting season expected April/ May 2020). Fruit production is then going to be measured again for two consecutive fruiting seasons in post-weeded conditions (April – September 2020 and October 2020 – April 2021) to study the effects of weeding on fruit production of native plants. Weed removal is going to be carried out with machetes by a two-man team. Because the canopy is not very tall (6 – 9 m) and tree trunks are generally between 5 – 8 cm DBH, only the individuals < 8 cm DBH of the most abundant invasive plants will be removed, including: *Ardisia crenata*, *Flacourtia* sp., *Justicia* sp., *Clidemia hirta*, *Ligustrum robustum*, *Litsea glutinosa*, *Litsea monopetala*, *Ossaea marginata* and *Psidium cattleianum*. Stems will be cut as low to the base as possible and the stems will be removed from the plots.

Seedling recruitment

Additionally, 10 random 0.5 m by 2 m plots will be allocated within every 10 m by 10 m plot to measure seedling mortality and establishment. All exotic and native seedlings will be counted and ground cover (%) per species will be estimated before weeding activities take place. These plots will be reassessed every three months after weeding to measure seedling mortality and establishment and changes in seedling composition and cover. Weeding is likely to increase native seedling establishment and cover by releasing native seedlings from competition (Baider and Florens, 2011).

Preliminary results:

Ecology of *M. fascicularis*

Activity patterns and fruit availability

We collected a total of 737 scans (mean \pm SD = 2 ± 1 individuals per scan; range = 1 – 9 individuals) amounting to 61.4 of contact hours (mean \pm SD = 4.7 ± 1.8 hours per day) spread

across 13 days in both December 2019 (7 days) and February 2020 (6 days). Our study troop was almost exclusively arboreal, spending 98% of their time in trees. Troop members were only recorded on the ground when moving uphill, when foraging on cliffs or in dwarf forest or when foraging near the forest edge to reach certain plant species. The macaques spent largest proportion of the time feeding (53%), followed by moving (20%) and resting (17%). Activity patterns did not differ greatly between December and February (Fig. 5). Pine cone made up large proportions of the diet in both December (44%) and February (62%), followed by fruit (44% in December and 35% in February, Fig. 5). Other food sources included leaves (2.8%), flowers (1.2%) and insects (1.2%). Out of the insects, a large proportion was made up of a native cicada *Abrieta brunnea* (44%). The overall use of *Pinus nigra* and consumption of pine cone increased slightly in February compared to December (Fig. 5), but the daily use of pine did not differ significantly between months (Mann-Whitney *U*-test: $P = 0.1$). Of the fruits *M. fascicularis* fed on, *Litsea* spp. constituted the majority (86%), followed by *Flacourtia indica* (9.2%) and *Ligustrum robustum* (1.1%). Native fruits only comprised a very small percentage of the diet (0.3%) and consisted only of *Eugenia pyxidata*.

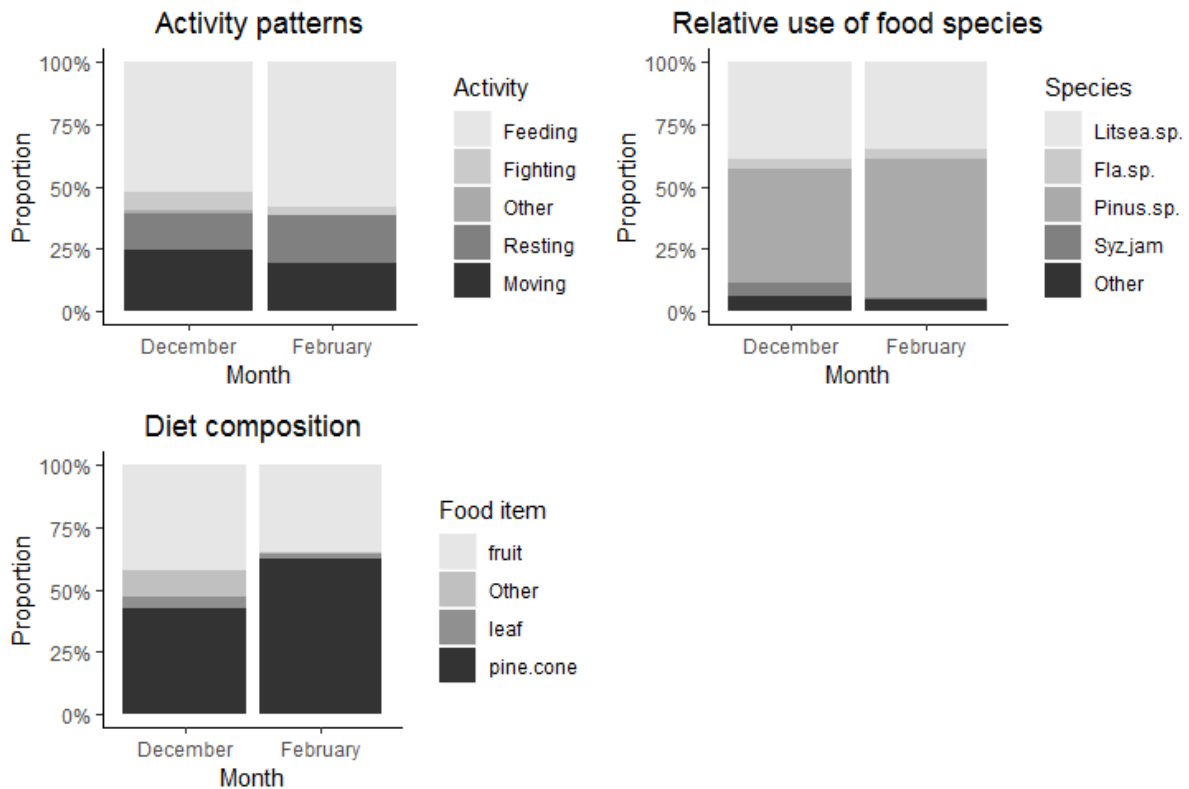


Figure 5: Proportion of time *M. fascicularis* was engaged in different behavioural activities (top left), proportion of time *M. fascicularis* spent feeding on different plant species when feeding on plant items (top right) and proportion of time *M. fascicularis* spent feeding on various food items.

We recorded 887 trees belonging to 38 species along our phenology transects (Appendix 1). Fruit availability was lower for *Litsea* spp. in February 2020 than in December 2019 but overall fruit availability increased (Tab. 1). This increase in the overall availability of fruit was not reflected by the proportion of fruit in the diet, since *M. fascicularis* mainly fed on

Litsea spp. that comprised the majority of the fruits in the diet during both months (86%). The low number of native fruits compared to exotic fruits in the diet was also reflected by the low FAI_{native} compared to the high FAI_{exotic} (Tab. 1). During all months, *Litsea* spp. was the only species providing ripe fruits. Furthermore, fruit yield was low for both native and exotic species (Tab. 2).

Table 1: Monthly fruit availability index (FAI) scores for a few canopy species in our study site that were included in *M. fascicularis* diet: native *Eugenia pyxidata* (Eug pyx), invasive *Flacourtia indica* (Fla ind) and invasive *Litsea* spp. (Lit sp.). Additionally, the monthly FAI scores for native, exotic and total plant species are provided.

Species	December	January	February
Eug pyx	414	414	166
Fla ind	1383	4069	8219
Lit sp	10137	4919	2683
Native	2642	4966	6929
Exotic	12961	12220	15193
Total	15602	17185	22122

Table 2: Fruit yield median, *IQR* and range for a few canopy species in our study site that were included in *M. fascicularis* diet: native *Eugenia pyxidata* (Eug pyx), invasive *Flacourtia indica* (Fla ind) and invasive *Litsea* spp. (Lit sp.). Additionally, median, *IQR* and range have been provided for native, exotic and total fruit yield.

Species	January		February	
	median \pm <i>IQR</i>	range	median \pm <i>IQR</i>	range
Eug pyx	0 \pm 4	0 - 16	0 \pm 0	0 - 4
Fla ind	40 \pm 8	0 - 180	90 \pm 70	90 - 1120
Lit spp.	0 \pm 0	0 - 280	0 \pm 0	0 - 300
Native	0 \pm 0	0 - 200	0 \pm 0	0 - 2800
Exotic	0 \pm 0	0 - 300	0 \pm 0	0 - 1320
Total	0 \pm 0	0 - 300	0 \pm 0	0 - 2800

Fruit damage

Fruit consumption and damage was quantified for a total of 53 feeding events spread across 13 days from December 2019 until February 2020 (total feeding time = 6.6 hours). When *M. fascicularis* fed on fruits during these sessions, they exclusively ate or dropped unripe fruits, except for *Litsea* spp (27.5% of dropped and eaten fruits were ripe). *Macaca fascicularis* ate more ripe than unripe *Litsea* fruits (63% ripe), but dropped large quantities of unripe fruit while feeding (Tab. 3). Moreover, *M. fascicularis* generally dropped large quantities of intact fruits (total n = 1430, Tab. 3, Fig. 6).

Table 3: Median and *IQR* for number of fruits, flowers and leaves eaten (either spat out, partly eaten or destroyed) and for number of fruits and branches dropped by a single macaque when feeding on the following plant species: *Eugenia pyxidata*, *Ficus reflexa*, *Flacourtia indica*, *Litsea* spp., *Pinus nigra* and *Syzygium jambos*. The status (native = N or exotic = E), size of

the fruits (s = diameter < 1 cm, m = diameter ≥ 1 cm but ≤ 3 cm, l = diameter > 3 cm) number of sampled feeding events (n) and mean feeding time in minutes with SD (t) are also given for every species.

Species	St atu s	Si ze	n	t (mean ± SD)	Eaten (median ± IQR)			Dropped (median ± IQR)	
					Fruits	Flowers	Leaves	Fruits	Branche s
Eug pyx	N	m	1	16	61	-	-	7	-
Fic ref	N	s	1	2	-	-	5	2	-
Fla ind	E	m	3	5.3 ± 1.5	-	-	-	5 ± 13	-
Lit spp.	E	s	8	6.6 ± 5.3	1 ± 8	-	-	25 ± 37	1 ± 3
Pin nig ¹	E	L	8	9.3 ± 6.2	4 ± 3	-	-	1 ± 1	-
Syz jam	E	m	2	4.5 ± 0.7	5 ± 5	1 ± 1	-	2 ± 2	1 ± 1

¹ The cones of *P. nigra* have been counted as fruits in this table.



Figure 6: Dropped and eaten unripe fruits of *Syzygium jambos*, eaten shoots and unripe fruit of *Ficus reflexa* and dropped unripe fruits and eaten leaves of *Litsea* spp. (A), dropped branches and unripe fruits of *Flacourtia indica* (B), eaten unripe fruits of *Eugenia pyxidata* (C) and eaten and dropped pine cone of *Pinus nigra* (D). Picture A represents three separate

feedings sessions with one macaque of 6, 2, and 3 min, pictures B and D each represent one feeding session with two macaques of 6 and 17 min respectively and picture C represents one 16 min - feeding session with one macaque.

Home range and fruit availability

Home range size differed between December and February (18.4 and 6.4 ha respectively, Fig. 7), giving a mean home range of 12.3 ha.

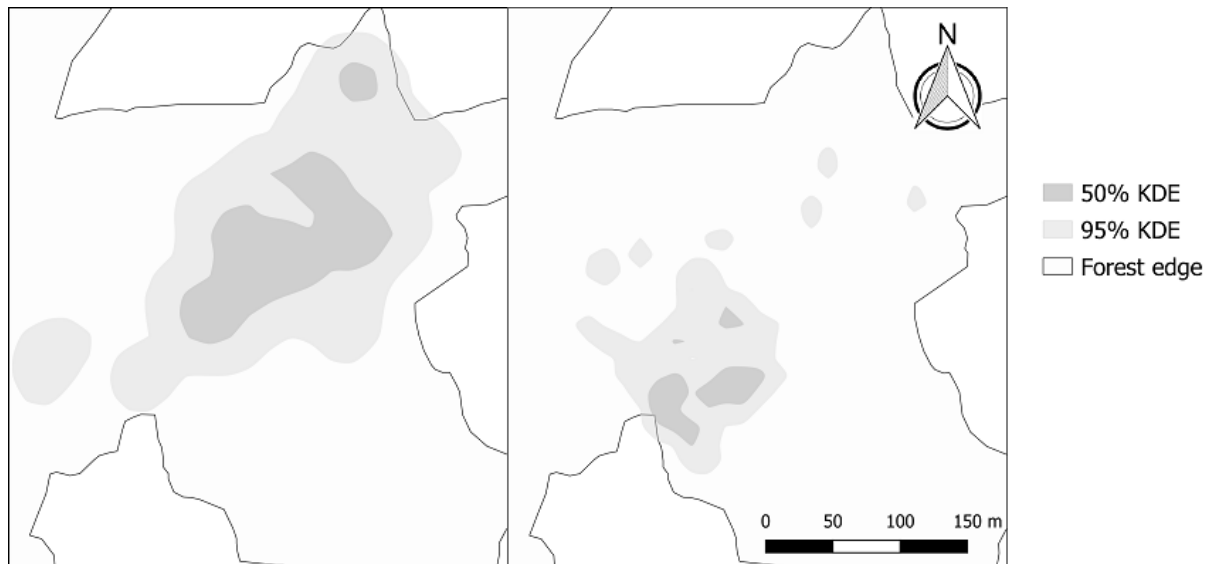


Figure 7: Monthly home ranges of the study troop during December 2019 (left) and February 2020 (right), represented by the 95% KDE. Core areas are represented by the 50% KDE.

Paths lengths were significantly longer in December (median \pm IQR: 61.1 m \pm 67.4 m) than in February when fruit availability was higher (28.8 m \pm 76.1 m, Mann-Whitney *U*-test: $P = 0.01$).

Population estimate

Recent habitat maps have not been acquired yet. Therefore, we used the same areas within and outside of 1 km from cultivation used for the population estimate in Bertram (1994). This estimate should be treated with caution, as a lot of forest habitat has been converted since 1994. The density of macaques in our study area is obtained by dividing the troop number (at least 19 troop members) by the home range (12.3 ha), giving us 1.6 macaques per ha. Bertram estimated the total habitat available to macaques at 383 km². Of the total habitat, 258 km² are within 1 km of cultivation. Therefore, areas within 1 km from cultivation contain: 258 * 100 * 1.6 = 41280 macaques. Areas outside of 1km from cultivation contain: 125 * 100 * 0.8 = 10000 macaques. As a result, we arrive at a total population of 51280 macaques.

Weeding experiment

Fruit production has been monitored on a weekly basis since October 2019. The main fruiting season will come to an end around April 2020. So far, all species selected for this study, except for *Calophyllum tacamahaca* and *Sideroxylon puberulum*, are flowering or fruiting. In the case of *S. puberulum*, it is likely that no flowers will be produced since this species flowered in our study site in January 2019 (Reinegger et al., 2020 under review).

Furthermore, only *E. pyxidata*, *Syzygium duponti* and *S. mauritianum* have produced fruit so far. *Aphloia theiformis*, *Labourdonnaisia calophylloides* and *Psiloxylon mauritianum* lost large quantities of flowers, indicating that these species will not produce any fruit this season. This could be a result of a lack of pollinators or soil nutrient competition with invasive plants. For *E. pyxidata*, almost all fruits recorded in our seed traps were eaten at an immature stage by *M. fascicularis* (Fig. 8). Footage from camera traps (23-10-2019 until 2-11-2019) indicates that *M. fascicularis* was the only animals feeding in the tree and also picked and dropped fruit intact (Fig. 8). The macaques mainly consumed the fleshy portion that is closest to the pedicel and drop the part closest to the pistil and petal remains (Fig. 8, right). This finding is also supported by our behavioural data. We expect the fruiting season to come to an end around April 2020 and will then proceed with weeding activities.



Figure 8: *Macaca fascicularis* feeding on immature fruits of *Eugenia pyxidata* (left and middle). Intact immature *E. pyxidata* fruits and immature *E. pyxidata* fruits eaten by *M. fascicularis* (right).

Discussion

Activity patterns and behaviour

Our study troop spent the majority of its time feeding (53%) and moving (20%). This activity pattern is similar to what Sussman et al. (2011) found in their study site (32% feeding and foraging, 25% moving and travelling), most likely because food sources are patchily distributed in all disturbed forests across the island. As a result, *M. fascicularis* has to spend most time travelling and foraging to obtain sufficient nutrients every day. Similar patterns were also recorded in disturbed forest on the Malay Peninsula (MacKinnon and MacKinnon, 1980) and Borneo (Mohammad and Wong, 2019). It is common for macaques in fragmented and disturbed habitat to spend the majority of the time moving and foraging (Sha and Hanya, 2013).

Moreover, *Macaca fascicularis* is considered a “refuging species” throughout its range, returning to a central sleeping site every night (Van Schaik et al., 1996; Sussman et al., 2011).

Our study troop also showed typical ‘refuging’ behaviour and their sleeping area was located within a convergence zone of the three largest gullies in between Calebasses mountain and Mariannes. Contrarily, Sussman et al. (2011) found that *M. fascicularis* uses cliffs as sleeping area in the Southwest of Mauritius. Therefore, our troop behaved more similar to *M. fascicularis* in its native range, where sleeping sites are usually located around rivers (Wheatley, 1980; Van Schaik, 1996). Our troop also differed from the troops studied by Sussman et al. (2011) as our troop members spent most of their time in trees (98%) instead of on the ground. This mostly arboreal nature is shared with *M. fascicularis* populations in most of Southeast Asia, especially in places where they are sympatric with *M. nemestrina*: 71% of time in the trees recorded by Crocket and Wilson (1980) and 97% recorded by Wheatley (1980). The availability of contiguous vegetation in our study site may have allowed the macaques to stay in trees, contrary to study site used by Sussman et al. (2011) that consisted mostly of shrubland and savannah. These findings highlight spatial variation in behaviour and ecology of a population of introduced *M. fascicularis* and the ability of *M. fascicularis* to adapt to a wide variety of disturbed habitats. Additionally, our findings show that when given a choice, *M. fascicularis* may prefer ‘refuging’ near moving water bodies, since steep cliffs were also present in our study site.

Diet composition

The proportion of fruits in the diet of *M. fascicularis* (35% - 44%) was very similar to previous studies on *M. fascicularis* in Mauritius (38%, Sussman et al., 2011). The low proportion of native compared to exotic fruits in the diet was reflected by the low native compared to exotic FAI. However, the most important food source was pine cone. The availability of pine cone was not measured, but it appeared to be a consistent resource throughout the study period. If we assume that pine cone is more difficult to digest than fruit and is thus less nutritious, we can consider it a ‘fallback food’ and would expect the time *M. fascicularis* spends feeding on pine cone to decrease as fruit availability increases. However, the proportion of pine cone in the diet did not decrease during February, despite the higher fruit availability. This may be explained by the fact that the fruits of all species except *Litsea* spp. were still immature. However, home range and daily path lengths decreased significantly, suggesting that *M. fascicularis* may have exploited higher local fruit availability. This indicates that *M. fascicularis* may use energy maximising strategies during periods of low fruit availability to obtain the preferred fruit resources. Nonetheless, we would have to demonstrate that fruit is a preferred resource first. Therefore, it will be important to continue following the troop until the end of the year so that Spearman’s Rank correlation coefficients can be calculated between monthly FAI and diet composition. Additionally, it will be valuable to measure pine cone availability. This is likely to reveal clearer dietary patterns and provide additional information on food preference. The dietary patterns of our troop may be similar to howler monkeys in Argentina (*Alouatta* spp.), which are known to exploit pine cone during periods of fruit scarcity (Agostini et al., 2010). *Alouatta* spp. and *M. fascicularis* both persist in highly disturbed forests (Crocket, 1998) and have some of the highest seasonal dietary variability among primates (Chapman and Chapman, 1990), emphasizing their opportunistic and adaptive abilities. However, this is the first time that *M. fascicularis* has been reported to feed predominantly on pine cone. Furthermore, our study suggests that potential fruit scarcity

can lead to almost exclusive consumption of unripe fruit and thus ineffective seed-dispersal by macaques.

Ecosystem impact

Macaca fascicularis ate exclusively unripe fruit for all species except *Litsea* spp. Quantification of eaten and dropped fruits during feeding events revealed that *M. fascicularis* mostly ate ripe *Litsea* fruits and great numbers of unripe intact fruit were dropped. Dropping intact unripe fruit was common for all the plant species *M. fascicularis* fed on. The low median fruit yield compared to the large fruit yield range of most species in *M. fascicularis*' diet showed there is high variability in fruit production and that the majority of trees produce very little to no fruit. Even though visual estimation of fruit yield can be inaccurate for some species because of 'hidden' fruits (Chapman et al., 1992), the difference between few and many fruits could easily be distinguished for all species along our transects. Therefore, the high median number of fruits that *M. fascicularis* ate and dropped for some of these species suggests that a single macaque can easily deplete fruit on a tree within a single feeding event. However, we have yet to detect *M. fascicularis* feeding on other native fruits besides *E. pyxidata*. Fruit availability is expected to increase even further as many species have only recently started producing fruits. However, failing to detect consumption of native fruits has likely been a result of insufficient habituation of the study troop, since the macaques were disproportionately nervous around the researcher in the dense, low canopy native forest compared to the higher canopy mixed pine forest. Feeding observations could barely be made because of the poor visibility. As a result, feeding in native forest was generally underrepresented in our data. A camera trap mounted on an *E. pyxidata* replicate for our weeding experiment also showed that *M. fascicularis* fed on these trees more frequently than we recorded. Therefore, it will be important to continue this study until the end of the year in order to assess the complete diet.

Nevertheless, *E. pyxidata* is a good example of probable native resource depletion by *M. fascicularis*. This species produces little fruit (median = 0, range = 0 – 16) and is scarce in the study site (Appendix 1). Despite the fact that some *E. pyxidata* individuals may produce much larger quantities of fruit that fall outside of our fruit yield range (n = 68) and the number of eaten fruits is likely to vary, our results suggest that a single macaque is able to deplete all fruit on an average *E. pyxidata* individual within minutes. Given that *M. fascicularis* feeds 53% of the day, it is likely that scarce *E. pyxidata* fails to produce ripe fruits because of *M. fascicularis*' exclusive consumption of unripe fruit. As a result, the endemic *Pteropus niger*'s diet is restricted, since *Eugenia* spp. are included in its diet (Florens et al., 2017; Reinegger et al., 2020 under review) and it is known to eat mostly ripe fruits. Moreover, reproduction of *E. pyxidata* is halted.

Macaca fascicularis had a number of other impacts on the native forests and its inhabitants. Numerous young shoots of native *Ficus reflexa* and endemic *Ficus mauritiana* were sometimes consumed. However, the low frequency at which this occurred and the limited number of shoots that were consumed during a feeding event suggest that this may not have a great impact on plant growth. Nevertheless, feeding observations in native forest were underrepresented in our study and thus the frequency of feeding on these shoots may be

higher. Additionally, both of the *Ficus* spp. are scarce in the study site and even infrequent feeding on shoots may limit plant growth. Mauritian native trees have evolved in the absence of mammalian herbivores while the only endemic herbivores on the island were not able to reach the arboreal foliage (Cheke and Hume, 2008). Therefore, it is likely that native trees lack herbivore defences such as enhanced recovery after foliage damage. This is illustrated by the overall slow growth of the Mauritian native flora (Virah-Sawmy et al., 2009). Furthermore, *M. fascicularis* fed on *Abrieta brunnea* (Orion, 1954), a native cicada in our study site that seemed abundant. The macaques were very skilled at chasing and catching these cicadas. The conservation status of this species is unknown, but *M. fascicularis* may limit their numbers through predation.

Home range and troop size

The mean home range found during our study (12.3 ha) was much smaller than what Sussman et al. (2011) found for his study troops (57 and 117 ha). However, these troops were much bigger in size (85 and 72 individuals respectively) than ours (19 individuals). If we divide the larger troop sizes by our troop size and multiple it by our home range we get a home range that is more similar (55.0 and 46.6 ha) to the home ranges estimated by Sussman et al. (2011). Furthermore, our home range is based on only two months of data and is likely to show more variation later during the year. Additionally, the troop often split into subgroups and remerged again during the day multiple times. This fissure-fusion pattern is common for *M. fascicularis* in Mauritius (Sussman et al., 2011). Therefore, the home range may be even larger than indicated in our study because subgroups typically foraged in different areas. This is most likely a result of the mosaic character of disturbed habitats, where different resources are patchily distributed (Sussman et al., 2011). Foraging as a single troop may prevent the macaques from obtaining sufficient resources.

Furthermore, troop size could have been underestimated due to the dense vegetation and limited visibility of moving individuals. Additionally, no distinction between subgroups could be made. While counting troop members, some individuals had often already split from the group. Vocalizing individuals in the distance during troop counts suggest that the troop may have had more members.

Population estimate

Our population estimate (51280) was a higher than the previous estimate (41670). This is mainly explained by the high macaque density obtained during our study compared than the density used by Bertram (1994). Nevertheless, it is important to treat this population estimate with caution, since suitable forest habitat is likely to have decreased since 1994. Additionally, macaques have been frequently observed near urban areas in the last few years, sometimes even away from suitable forest habitat. This suggests that *M. fascicularis* may have managed to establish in isolated patches of shrubland and woodland outside of major forest areas. Furthermore, the density used in our estimate may actually be bigger or smaller depending on how home range varies throughout the year and the number of troop members we missed during the counts. Therefore, it is important to continue this study until the end of the year and estimate the total area of suitable habitat with recent habitat maps. Moreover, to obtain a better estimate, it would be valuable to habituate additional macaque troops in other areas and

see how these differ in home range and troop size. Nevertheless, our findings indicate higher macaque densities than in Bertram (1990), indicating that the population most likely increased.

Implications for conservation of *P. niger* and native forests

Our findings suggest that native fruit availability in Mauritius may be scarce, given that the majority of fruits in *M. fascicularis* diet were unripe. Additionally, a large proportion of the diet was made up of pine cone while native fruit yield was low. Furthermore, our findings indicate that a single macaque can deplete unripe fruits on native trees within minutes. Since ripe fruit was not detected for any species except *Litsea* spp. while assessing both the phenological state of trees and diet composition of *M. fascicularis*, we have an indication that many fruits (both exotic and native) are limited to *P. niger*. Additionally, the macaque density obtained during this study is higher than in previous studies, suggesting that the populations could have increased. Our findings indicate that native forests cannot support such high densities of *M. fascicularis*. Therefore, it is possible that *M. fascicularis* halts native plant regeneration through consumption of unripe fruits and limitation of fruits to *P. niger*. However, it will be crucial to demonstrate that *M. fascicularis* prefers fruit over pine cone to provide clear evidence for fruit scarcity in our study site.

One last note: macaque tracking vs. habituation

Initially, we started this study by capturing and radio-collaring (MI-2, Holohill, USA; 110 g in weight) four adult macaques (three females and one male) with assistance from the local macaque breeding company Noveprim Ltd. Red hair dye was applied to both flanks so that tagged individuals could be visually identified from a distance. The macaques were then radiotracked from the ground with a three-element Yagi antenna and receiver (Sika Biotrack, US). However, both trapping and collaring procedures resulted in a great setback, since the collared macaques became terrified of people. The location of their sleeping site was discovered through radiotracking, but contact could barely be established in the dense vegetation for over two months. The collared macaques would run off when hearing the sounds of the approaching researcher, often before the researcher could see the macaques. Additionally, we discovered that the collared individuals were foraging alone as the rest of the troop was encountered coincidentally while trying to find the collared macaques. The radio signals indicated that the collared individuals were nowhere near the rest of the troop. The rest of the troop allowed the researcher to come within 20 m to 40 m. These macaques were then selected as study troop and their sleeping site was located by successfully following them for an entire day. Remarkably, the sleeping site of the four collared individuals was located in a different area than the sleeping site of the study troop, but still within the study troop's home range. On the day the macaques were trapped and collared, it appeared they were clearly part of the troop, as other macaques, were nervously watching in the surrounding trees and making alarm calls. No other troops have been encountered in the study area. Therefore, we believe that collaring the macaques may have resulted in exclusion from the troop. The collared macaques were also caught on camera trap (Fig. 9), showing that they still utilized part of the study troop's home range. In February 2020 the signals were checked again while following

our study troop, showing that the collared individuals were still foraging by themselves. This indicates possible negative consequences of radiocollaring primates for behavioural studies.



Figure 9: Radio-collared female caught on camera trap in *Eugenia pyxidata* in November.

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Appendices

Appendix 1: Plant species recorded along our phenology transects. Status (native or exotic) and total number of recorded stems (DBH \geq 5 cm) across all three transects are also provided for every species.

Family	Species	Status	Nr. of stems
Achariaceae	<i>Erythrospermum monticolum</i>	Native	23
Aphloiaceae	<i>Aphloia theiformis</i>	Native	10
Apocynaceae	<i>Tabernaemontana persicariifolia</i>	Native	9
Burseraceae	<i>Canarium paniculatum</i>	Native	2
Calophyllaceae	<i>Calophyllum tacamahaca</i>	Native	6
Ebenaceae	<i>Diospyros sp. 1</i>	Native	2
Euphorbiaceae	<i>Securinega durissima</i>	Native	22
Lamiaceae	<i>Premna serratifolia</i>	Native	1
Lauraceae	<i>Cinnamomum camphora</i>	Exotic	1
	<i>Litsea sp.</i>	Exotic	103
Loganiaceae	<i>Geniostoma borbonicum</i>	Native	6
Malpighiaceae	<i>Hiptage benghalensis</i>	Exotic	1
Melastomataceae	<i>Memecylon cordatum</i>	Native	1
Moraceae	<i>Ficus mauritiana</i>	Native	4
Myrtaceae	<i>Eugenia elliptica</i>	Native	3
	<i>Eugenia pyxidata</i>	Native	14
	<i>Psidium cattleianum</i>	Exotic	347
	<i>Syzygium commersonii</i>	Native	2
	<i>Syzygium glomeratum</i>	Native	15
	<i>Syzygium jambos</i>	Exotic	112
	<i>Syzygium mauritianum</i>	Native	3
Oleaceae	<i>Ligustrum robustum</i>	Exotic	50
Phyllantaceae	<i>Margaritaria anomala</i>	Native	1
	<i>Phyllanthus sp.</i>	Native	1
Pittosporaceae	<i>Pittosporum senacia</i>	Native	4
Primulaceae	<i>Ardisia elliptica</i>	Exotic	8
Psiloxylaceae	<i>Psiloxylon maritimum</i>	Native	5
Rubiaceae	<i>Danais fragrans</i>	Native	1
Salicaceae	<i>Casearia coriacea</i>	Native	2
	<i>Flacourtia sp.</i>	Exotic	113
Sapindaceae	<i>Molinaea alternifolia</i>	Native	1
Sapotaceae	<i>Labourdonnaisia glauca</i>	Native	1
	<i>Mimusops maxima</i>	Native	2
	<i>Sideroxylon puberulum</i>	Native	3
Stilbaceae	<i>Nuxia verticillata</i>	Native	1

Appendix 2: R-script for least-squared cross validation kernel density estimation (LSCV KDE) for estimating home range.

```
#####  
## clear workspace and set working directory ##  
#####  
# Clear plots  
if(!is.null(dev.list())) dev.off()  
# Clear console  
cat("\014")  
# Clean workspace  
rm(list=ls())  
# Set working directory  
setwd("C:/insert working directory")  
  
## attach data and explore  
mydata<-read.table("insert coordinate file name.txt",header=T,sep="\t")  
  
attach(mydata) # attatch the data into R  
  
####Install and load packages  
#install.packages("adehabitatHR")  
#install.packages("rgdal")  
#install.packages("rgeos")  
#install.packages("smoothr")  
library(adehabitatHR)  
library(rgdal)  
library(rgeos)  
library(smoothr)  
  
#####  
### Estimate home range (95% KDE) ###  
#####  
#make sure only three columns are included (Month, x, and y coordinates) for estimating  
home ranges  
HomeCalc <- mydata[, c("Month", "xcoord", "ycoord")]  
#set coordinates to right CRS (epsg: 3857 in this case)  
coordinates(HomeCalc) <- c("xcoord", "ycoord")  
proj4string(HomeCalc) <- CRS("+init=epsg:3857" )  
  
#calculate kernel density with least squares cross validation as smoothing parameter  
kernel.lscv <- kernelUD(HomeCalc, h = "LSCV") # Least square cross validation  
image(kernel.lscv) # plot  
  
#get area for 95% kernels  
homecalc.kernel.poly <- getverticeshr(kernel.lscv, percent = 95)  
print(homecalc.kernel.poly) # returns the area of each polygon  
#(the function's default input is in metres and output in hectares)  
  
#####
```

```
##### export shapefile #####
#####
#Export the 95% KDE (home range) and 50% KDE (core area) as shapefiles
#make polygons for 95% KDE
KDE95 <- getverticeshr(kernel.lscv, percent = 95)
#Now for 50% KDE
KDE50 <- getverticeshr(kernel.lscv, percent = 50)
#smooth the polygons with kernel smoothing to get rid of rough edges
KDE95 <- smooth(KDE95, method = "ksmooth")
KDE50 <- smooth(KDE50, method = "ksmooth")

#Write your 95% and 50% polygons into a shapefile that can be loaded into QGIS
writeOGR(KDE95, dsn = ".", layer = "KDE95", driver="ESRI Shapefile")
#A dsn value of "." will output the file in your working directory folder.
#Layer is the file name, driver is the type of file that is being made.
#Repeat for the 50% polygon
writeOGR(KDE50, dsn = ".", layer = "KDE50", driver="ESRI Shapefile")
```