



Foraging Strategies of Invasive *Macaca fascicularis* may Promote Plant Invasion in Mauritius

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Abstract

The effectiveness of seed dispersal by frugivorous primates may vary between seasons and plant species, depending on foraging strategies. We investigated how foraging strategies of an invasive frugivorous primate (the long-tailed macaque, *Macaca fascicularis*) affect seed dispersal effectiveness (SDE) between native and invasive plants in Mauritius' native remnant forests. By collecting behavioural data on a group of partially habituated macaques via scan sampling from December 2019 until December 2020 (mean $19.2 \pm \text{SD } 7.3$ hours per month), we investigated seasonal patterns in diet, home range, and fruit availability to identify foraging strategies and determine fruit preference. We simultaneously assessed SDE for invasive vs native plants by quantifying native and invasive fruits consumed or dropped intact by macaques during feeding bouts ($n = 114$). Macaques fed increasingly on ripe invasive fruits and less on other food items as fruit availability increased, due to preference for invasive fruits and disproportionate availability of invasive vs native fruits. When fruit became scarcer, macaques had larger home ranges, increasingly fed on scarce unripe native and invasive fruits, and expanded their diet by eating orchard crops, indicating use of energy-maximizing strategies. Macaques consumed more native than invasive fruits when unripe and commonly destroyed seeds of native fruits, indicating higher SDE for invasive vs native plants. Higher discard rates of unripe compared to ripe fruits further reinforced these differences in SDE. Our results highlight potential facilitation of plant invasion by an invasive primate, due to foraging strategies shaped by the availability of invasive fruits.

Keywords Invasive primates · Invasive frugivores · Biological invasions · Oceanic island · *Macaca fascicularis* · Seed dispersal

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Introduction

Optimal foraging theory predicts that animals consume low-quality food items increasingly as the abundance of preferred high-quality food items decreases (MacArthur & Pianka, 1966; Pyke, 1984). Therefore, seasonal changes in availability of preferred foods often influence foraging strategies of animals, including frugivorous primates (Garber, 1987). Ripe fruits are typically preferred foods for frugivorous primates (Marshall & Wrangham, 2007), as they are high-quality and high-energy food sources that are easy to digest (Garber, 1987; Harrison, 1984; Lambert, 2007). Consequently, frugivorous primates commonly adjust foraging strategies depending on fruit availability. When fruit becomes scarcer, frugivorous primates usually increasingly consume mature leaves, flowers, immature fruits, and seeds (Harrison, 1984; Nagy-Reis & Setz, 2017; Terborgh, 1983). These foods are often considered 'fallback foods' (Marshall *et al.* 2009), because they are less profitable than ripe fruits (e.g., due to lower digestibility, presence of toxins, or longer handling time) (Garber, 1987; Lambert, 2007). Furthermore, when fruits become scarcer, primates may range further to obtain a sufficient amount of their base diet due to low concentrations or patchy distribution of suitable food sources (Hall, 1962), an example of an energy-maximizing strategy (Harrison, 1984). They may also use energy-minimizing strategies in which animals range less far and increasingly forage on abundant low-quality 'fallback foods' (Nagy-Reis & Setz, 2017).

Such foraging strategies may cause seasonal variation in seed dispersal effectiveness (SDE) of frugivorous primates (Chapman & Russo, 2006), both in terms of quantity (number of seeds dispersed) and quality (probability that a viable dispersed seed survives handling, germinates and produces a new adult) (Schupp *et al.*, 2010). Quantity is affected by the number of consumed fruits (Schupp *et al.*, 2010), which often varies seasonally in frugivorous primates (Terborgh, 1983). Quality is affected in part by the type of fruit-handling behaviour and seed-dispersal distance. For example, seed swallowing or seed spitting are more likely to contribute to successful seed dispersal (Gross-Camp & Kaplin, 2011), whereas dropping intact fruits without removing the pulp (increasing the risk of fruit rot) (Traveset, 1998) and crushing seeds will probably hinder seed dispersal (Schupp *et al.*, 2010). Moreover, seed dispersal over bigger distances reduces distance- and density-dependent mortality and may thus increase establishment and survival success of seeds (Schupp *et al.*, 2010). The ripeness stage at which the fruit is handled can also affect dispersal quality, as ripeness is generally an indicator of seed germination success (Sumner & Mollon, 2000). Therefore, frugivorous primates may be less effective dispersers during periods of fruit scarcity, because the frequency of unripe fruit/seed predation can increase (Chapman & Russo, 2006). In contrast, primates may become more effective seed dispersers when fruit is scarce if they increase their home range, potentially increasing seed dispersal distances (Chapman & Russo, 2006). However, seed dispersal distance will largely depend on the fruit-handling behaviour (Chapman & Russo, 2006).

Foraging strategies may also lead to variation in SDE between plant species, as different fruiting species have an unequal chance of selection: fruit choice of

vertebrate frugivores generally depends on fruit traits (Crestani *et al.*, 2019), crop size (Ortiz-Pulido *et al.*, 2007), spatial aggregation of fruiting trees (Manasse & Howe, 1983), and the timing of fruiting of a tree relative to conspecifics or other plant species (Gleditsch *et al.*, 2017). Variation in SDE between plant species may be problematic in areas where frugivorous primates are invasive (Jones *et al.*, 2018). Even though in some cases invasive frugivores can provide important dispersal services to native plants (Vizentin-Bugoni *et al.*, 2019), invasive frugivores often mainly disperse invasive plants and/or predate seeds of native plants (López-Darias & Nogales, 2008; Martin-Albarracín *et al.*, 2018), due to factors such as disproportionate availability of invasive compared to native fruits, or attractive fruit traits of invasive plants (Bitani *et al.*, 2020; Chimera & Drake, 2010). This may be especially common on oceanic islands, where invasive plants are typically numerous and highly abundant (Denslow, 2003) and may produce more profitable fruits than native plants (e.g., higher energy, protein, or lipid content), potentially due to the limited spectrum of fruit traits in island floras (Kueffer *et al.*, 2009). Consequently, invasive primates may use foraging strategies that promote plant invasion on islands. Remarkably, seed dispersal by invasive primates has barely been addressed (Oliveira-Silva *et al.*, 2018), let alone on islands (Kemp & Burnett, 2003).

The long-tailed macaque, *Macaca fascicularis* (Cercopithecidae), is a primate native to Southeast Asia (IUCN status: Vulnerable) (Eudey *et al.*, 2020), where it is often highly frugivorous and conforms to predictions from optimal foraging theory (Ruslin *et al.*, 2019; Yeager, 1996). It is also an example of a primate that has been introduced to oceanic islands globally (Global Invasive Species Database, 2019), including Mauritius, where it was introduced around the seventeenth century (Sussman & Tattersall, 1986). Even though *Macaca* spp. are considered valuable seed dispersers in their native range (Albert *et al.*, 2013b; Sengupta *et al.*, 2020; Tsuji, & Su, H. -H., 2018), in Mauritius long-tailed macaques may mainly disperse invasive plants. Invasive plants dominate most forest habitats and are a major threat to native forests (Florens *et al.*, 2016; Florens *et al.*, 2017; Strahm, 1993), which now cover only 4.4% of their original extent (Hammond *et al.*, 2015). The macaques are known to feed on the fruits of abundant invasive plants (Sussman *et al.*, 2011), which often have fruit traits that are generally preferred by long-tailed macaques (sweet and acidic, Ungar, 1995) (e.g., *Psidium cattleianum*) and/or are consumed by long-tailed macaques in their native range (e.g., *Litsea glutinosa*; Azzahra, 2017). In contrast, the macaques appear to act mainly as a seed predator for native plants (Baider & Florens, 2006; Krivek, 2017; Reinegger *et al.*, 2021), indicating that native fruits may mainly serve as 'fallback food'.

These foraging patterns would create quantitative and qualitative differences in SDE between invasive and native plants that could facilitate plant invasion. Therefore, we aimed to investigate foraging strategies used by macaques in Mauritius and how these strategies affect SDE of macaques for invasive and native plants in a degraded native remnant forest. We first identified foraging strategies by evaluating the relationships between seasonal fruit availability, diet composition, and ranging patterns of macaques. As ripe fleshy fruits are a high-quality and often preferred food source for frugivorous primates (Marshall & Wrangham, 2007), we

first hypothesized that macaques adjust foraging strategies depending on seasonal availability of fleshy fruit (Lucas & Corlett, 1991; Yeager, 1996). We predicted that during high fruit availability, macaques would feed on more clumped/abundant ripe fleshy fruits and consequently would have a smaller home range size. Conversely, during low fruit availability, macaques would increasingly consume more scattered 'fallback' foods (e.g., flowers, unripe fruits, and leaves) and increase their home range size as a result. Thereafter, we measured seasonal SDE of macaques for native and invasive plants in both qualitative and quantitative terms: determining the fruit handling methods used by macaques, and quantifying the consumption and drop of invasive and native ripe vs unripe fruits. We hypothesized that macaques disperse invasive plants more effectively than native plants, because invasive plants are disproportionately abundant in Mauritius (Florens *et al.*, 2016) and may possess fruits that are more attractive or profitable to macaques than native fruits (Kueffer *et al.*, 2009). Therefore, we predicted macaques would consume more ripe fruits of invasive vs native plants. Additionally, we hypothesized that the probability of fruit rejection (drop of intact fruit) by macaques is affected by fruit maturity and availability, because primates are considered 'choosy' feeders that are more likely to reject unripe fruit when more appealing ripe fruit is available (Janson, 1996). We predicted that macaques would drop a higher proportion of unripe than ripe fruits intact during high fruit availability compared to low fruit availability.

Methods

Study Site

We conducted our study on Mt. Calebasses (-20.181203°S, 57.584498°E), a forest remnant in the north of Mauritius (Fig. 1) that contains a relatively rich native plant community (Reinegger, 2018) and is inhabited by four to five macaque groups (RR pers. obs.). The site is between 420 and 580 m asl and receives 1800–2200 mm of rainfall per year (Willaime, 1984). The forest consists of semi-dry vegetation at lower elevations and sub-humid vegetation at higher elevations. Moreover, the forest is extremely degraded at lower elevations, and mostly consists of a remnant pine plantation (non-native *Pinus elliottii*) and dense thickets comprising invasive *Flacourtia indica*, *Hiptage benghalensis*, *Ligustrum robustum*, *Litsea* spp., *Psidium cattleyanum*, *Rhamnus nepalensis* and *Syzygium jambos*. Most of these species were introduced for gardening and horticulture by the French during the eighteenth century (Cheke, 1987; Cheke & Hume, 2008). Except for *F. indica*, *P. cattleyanum*, all species occur in the native range of the long-tailed macaque.

Study Group and Habituation Process

We habituated a group of macaques occupying a steep, densely vegetated, north-west-facing slope on Mt. Calebasses during October–November 2019 (Fig. S1). We could not fully habituate the group to human observers during this period,

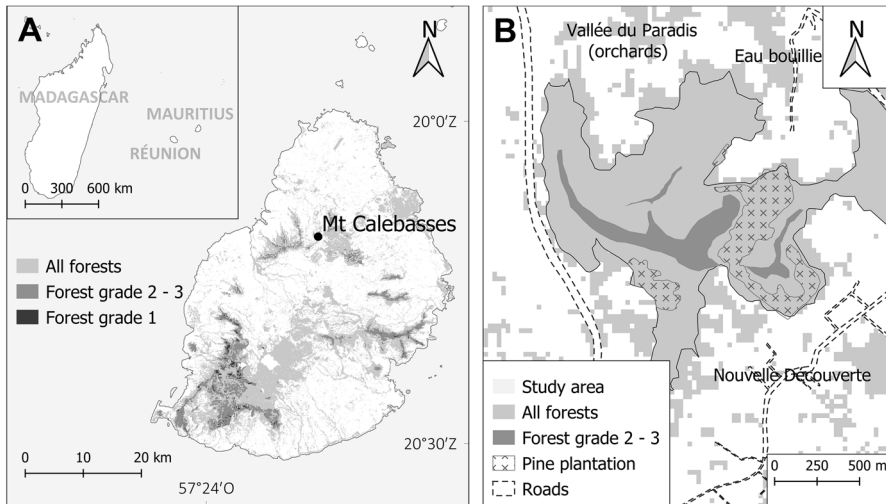


Fig. 1 Location of the study area (Mt. Calebasses) and distribution of forests in Mauritius (a) and close-up of the study area in Mt. Calebasses (b). *Forest grade 2–3* is forest with native plant cover $\geq 50\%$ but $\leq 75\%$ and *Forest grade 1* is forest with native plant cover $> 75\%$.

but by December 2019 we could approach to within 5–20 m of them and follow them consistently for 2–6 hours at a time. At this stage of the habituation process, we were able to collect data (cf. ‘partial habituation stage’; Gazagne, Hambuckers, *et al.*, 2020a). We could identify the group by three immature individuals that commonly foraged together and were the first to approach within 10 m of the researcher in the first 2 months and < 2 m after 4 months. Additionally, the group reused the same three sleeping sites from December 2019 until September 2020. On days that we lost our study group during the first 4 months, we revisited the sleeping sites in the early evening to confirm they had not changed sleeping sites. Individuals from the group also increasingly tolerated and ignored the researcher as our study progressed, eventually enabling us to follow the group in dense stunted vegetation at a 5–10 m distance from March 2020. In contrast, individuals from neighbouring groups ($n = 3$) remained very skittish and ran as soon as they noticed the researcher, making it impossible to follow these groups. Our group consisted of 19–23 individuals, made up of 1–2 adult males, 3–5 adult females and 12–16 immature individuals (sub-adult, juveniles, and infants). We could identify adult males and females based on differences in their physical features: adult females have ‘beards’ and protruding teats, whereas adult males are larger than adult females, have prominent genitalia and an often upwards curling moustache (lacking the ‘beard’ that is present in adult females) (Brotcorne, 2014; Jamieson, 1998). These features are much less pronounced in immature individuals (largely absent in infants and juveniles) (Brotcorne, 2014) and thus we were not able to clearly identify sex for most immature individuals. Group size may have slightly varied during our study due to migration of males. However, we could not detect migrations, because we had few opportunities to observe the

complete group and it was difficult to distinguish between individuals in the same age–sex class.

Data Collection

We followed the group for half a day 4 times a week from December 2019 until December 2020: either from the moment the macaques left their sleeping site (05:30–6:00) until 13:30, or from 11:00 until the macaques returned to their sleeping site (18:00–18:30), or until we lost the group for longer than 1.5 hours. We usually followed the group for 2 consecutive half-days in a row twice a week, spreading sampling effort equally across times of day (2 days 5:30–13:30, 2 days 11:00–18:30). We chose half-day intervals over full days (05:30–18:30) because the high topographical relief in the area combined with steep slopes made following the group very physically demanding. Furthermore, activity patterns of macaques in the southwest of Mauritius were very consistent throughout the day (Sussman *et al.*, 2011), suggesting that our chosen half-day interval can represent the whole day.

We recorded the study group's geographical position every 30 minutes with a handheld Global Positioning System (GPS) (eTrex 30x, Garmin; Olathe, KS) using the degrees and decimal minutes (DMM) format projection. Simultaneously, we collected dietary and behavioural data by scan sampling the group at 5-min intervals (Altmann, 1974), typically at 5–20 m distance from the group. We collected a total of 2764 scans over 75 days (mean = $3.1 \pm$ SD 1.8 hours per day) from December 2019 until December 2020 ($19.2 \pm$ 7.3 hours per month), excluding January 2020 (due to frequent cyclones and torrential storms). During scans, we observed each visible group member for 10–15 seconds to record its behaviour (2 ± 1 individuals per scan; range = 1–9 individuals). We noted different behaviours (moving, resting, feeding, and social interactions), but we only used feeding behaviour in our analyses. Feeding behaviour corresponded to 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, we recorded the first item that was consumed (pine cone, insect, fruit, leaf, bark, flower, egg, seed, grass, or crop). Whenever we could not clearly identify food items or a plant species (because of poor visibility), we recorded them as unknown.

Availability of Fruit and Other Plant Foods

To assess fruit availability within the home range of our study group, we first estimated tree density by marking all stems with diameter at breast height (DBH) \geq 5 cm along four vegetation transects. Two were oriented in the north–south direction and two were oriented east–west. Each transect was 2 m wide and 200 m to 400 m in length, covering a total area of 0.24 ha within the group home range, but outside of the pine plantation (Fig. 1b). Because the long-tailed macaque is an opportunistic feeder in its native range (Gumert, 2011) as well as in Mauritius (Sussman *et al.*, 2011), we included all tree and liana species present in the vegetation transects. However, we grouped invasive *Litsea glutinosa* and *Litsea*

monopetala together as *Litsea* sp., because it was difficult to distinguish between the two species (similar leaves, fruits, flowers, and fruiting periods). At the start of every month, we recorded the phenological state of all stems (1288 stems and 39 plant species, Table S1) along three transects (presence/absence of flowers and ripe and unripe fruits). Based on the percentage of crown area covered by fruits (visual estimation), we ranked trees on a 5-point scale where a score of 0 implies no fruits and scores of 1 (1–25%), 2 (26–50%), 3 (51–75%), and 4 ($\geq 76\%$) imply increasing percentages of crown area covered by fruits (Albert *et al.* 2013a). We also recorded flower cover using the same 5-point scale. The total fruit availability index (FAI) was then 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 (stems/ha), B_i is the mean basal area of trees of species i (cm^2/ha) and P_{im} is the mean score of fruit cover in species i in month m . This is then totalled for all species (n) in the phenology transects. We defined high versus low fruit availability periods as months with FAI values twice the standard error (SE) above versus below the mean FAI value across the entire study period. Months with FAI values in between the high and low values were classified as the medium fruit availability period. We used the same method to calculate FAI scores for invasive and native plant species independently. We also calculated an availability index for flowers (FAI), where P_{im} was replaced with the mean score of flower cover in species i in month m . Furthermore, during the first 2 months of the study it became apparent that pine cone was an important resource for the study group. Therefore, we also calculated a pine cone availability index (PcAI), by establishing a vegetation transect (2 m by 300 m) in the pine plantation (Fig. 1b) and recording monthly pine cone cover on trees using the same 5-point scale as for the FAI and FAI. We calculated the PcAI by multiplying B_{pine} by P_{pine} for every month. We could only record pine cone availability from March 2020 until December 2020.

Diet Composition

We obtained monthly diet composition by calculating the weighted monthly proportions of dietary scans macaques spent feeding on every food item and plant species to account for unequal daily sampling effort, using the formula from Harrison *et al.* (2009):

$$F_i = \frac{\sum (F_{ij} * W_j)}{\sum W_j}$$

Where F_{ij} is the daily number of scans for feeding on a particular food item or plant species i on day j , and W_j is the total number of dietary scans on day j .

Fruit Preference

We calculated fruit preference indices (FPI_i) for every plant species that macaques consumed fruits of to investigate preference among different fruits using the formula from Sengupta and Radhakrishna (2015):

$$FPI_i = \frac{f_i}{a_i}$$

Here, f_i is the weighted ratio of dietary scans that macaques spent feeding on the fruits of species i to the total number of fruit feeding scans in the period that species i was available, and a_i is the ratio of fruiting stems of species i to the total number of fruiting stems during the fruiting period of species i . A preference index of > 1 indicated that macaques preferred the fruit of the plant species.

Home Range

We used R to perform least square cross-validated fixed kernel density estimation (LSCV KDE) to estimate the monthly and annual home ranges (using package *ade-habitatHR* — Calenge, 2021), because it is one of the most widely used methods for home-range estimation and enables comparison with other studies (Albert *et al.* 2013a; Hanya *et al.*, 2020; Seaman & Powell, 1996). Based on the group location every 30 min, we used the 95% confidence region of the KDE to represent the home range and reflect the area associated with a 95% probability of finding the animal. Moreover, we calculated the 50% confidence region, reflecting the core area that is used disproportionately more by the animals than other areas of the home range (Rühmann *et al.*, 2019). We determined whether spatial autocorrelation of GPS locations was a problem by following the workflow from Calabrese *et al.* (2016) (using package *ctmm* — Fleming, 2021), because LSCV KDE relies on spatial independence of GPS locations. The results indicated some autocorrelation for locations separated by short time lags (0.5–6 hours). Therefore, we carried out autocorrelated kernel density estimation (AKDE, Fleming *et al.*, 2015) and compared its performance to the LSCV KDE by following the workflow from Noonan *et al.* (2019). The performances differed very little, but the AKDE estimate extended into open areas that our study group avoided (including motorways). Therefore, we concluded that LSCV KDE provided more accurate estimates of monthly home ranges and core areas.

We also assessed how well our GPS data represented the monthly home ranges by bootstrapping monthly estimates (as estimated by LSCV KDE) for different sample sizes (using package *rhr* — Signer & Balkenhol, 2015), because we collected an unequal number of GPS locations every month (range: 24–79). We plotted the bootstrapped home-range estimates against sample size to determine whether the sampling imbalance was a problem. Home-range estimates roughly approached an asymptote at around 30–40 GPS points for all months (Fig. S2). Therefore, a larger number of GPS points barely affected monthly home range estimates, so we included all GPS points. We exported the final monthly and annual home ranges

(including both the 95% and 50% KDE's) as shapefiles and mapped them in QGIS (QGIS Development Team, 2020).

We removed November 2020 from our dataset, because the group migrated to the north-western forest edges near the orchards in Vallée du Paradis during October 2020 (when forest fruit was scarce), where it remained until the end of our study period. The group did not travel to this area prior to October 2020. In November 2020 our group primarily fed on mango (*Mangifera indica*) around the orchards and agricultural fields, a resource that was not available in the area the group used prior to October 2020. Consequently, monthly home range in November was much smaller than in the other months outside of the high fruit availability period. Mean monthly home range outside of the high fruit availability period (December 2019 and July–December 2020) was 15.1 ha (SD = 7.1) and November was the only month under 12 ha (4.3 ha).

Seed Dispersal Effectiveness

We assessed SDE of macaques by opportunistically quantifying consumption and drop of ripe vs unripe fruits by macaques during feeding bouts using all-occurrence sampling (Lehner, 1992). We defined the start of a feeding bout as the moment that a macaque or a group of macaques started feeding in a tree (or clump of small trees of the same species, e.g., *P. cattleyanum*). We recorded the exact time when the macaques started feeding and the number of feeding individuals. We then randomly selected one feeding individual and observed it for as long as the individual fed on the same tree (or clump of small trees) to determine the fruit parts it was consuming (whole fruit, pericarp, seed). We also determined the state of ripeness of fruits (ripe/unripe), defined the size of the seed by length to allow comparison to other studies (small: maximum length < 5 mm; medium: ≥ 5 mm but < 10 mm; and large: ≥ 10 mm) (Traveset, 1998) and the type of fruit handling method used by macaques: 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 the fruit, 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). We also recorded exits and entries of individuals during group feeding bouts to determine the total number of individuals that had fed in the same feeding tree. We defined the end of the feeding bout as the moment when all macaques had left the feeding tree.

At the end of the feeding bout, we counted the discarded partly eaten pericarp of ripe and unripe fruits beneath the feeding tree to determine the number of consumed fruits. For plant species with small fruits that only contained a single seed, we counted spat-out or discarded seeds instead of discarded pericarp (e.g., *Litsea* spp.). We also counted the number of fruits dropped by macaques intact (either picked and discarded or accidentally dropped). To avoid counting fruits that had been dropped (both partly eaten and intact) during earlier feeding bouts, we distinguished between fresh and old dropped fruits. Older dropped fruits (0.5–2 hours after the end of the

feeding bout) were either discoloured (enzymic browning), had a sour and pungent smell (fresh fruit of most plant species have a neutral or sweet smell) and/or lost their original shape (became soft and wet), whereas fresh fruit that was counted or gathered shortly after the feeding bout (mean feeding bout duration = $7.4 \pm \text{SD } 5.6$ minutes) had barely browned and/or remained crisp. We determined these changes in fruit shape, colour, and smell by revisiting the feeding tree 0.5–2 hours after the feeding bout whenever the group remained close to the feeding tree after the feeding bout to check the dropped fruits again. When counting fruits after a feeding bout, we either counted fruits on site (only when possible within 2–3 minutes) or collected and stored in zip-lock bags so that they could be counted after field activities on the same day (Fig. S3). Since we could often not distinguish between fruits handled by different individuals on the same tree in dense vegetation, we divided the total number of consumed and dropped fruits by the duration of the feeding bout and the total number of feeding macaques recorded during the feeding bout, to estimate fruit consumption and dropped fruit per macaque per minute of the bout. This method was suitable for most canopy species with medium to large-seeded fruits. However, very small seeded fruits, such as those of *Ficus reflexa* and *F. rubra*, were sometimes swallowed whole, so quantification was limited for these species. Furthermore, seeds of *Litsea* sp. were too big to be swallowed, but the small fruits were often stored in the cheek pouches (Fig. S4). Therefore, for these species we could not count all eaten fruits.

Statistical Analyses

We used R (R Core Team, 2020) for all statistical analyses. To identify foraging strategies, we first examined whether the monthly weighted percentage of scans spent feeding on different food items (e.g., fruits, flowers, and crops) was related to monthly availability of different food items (e.g., FAI and FIAI) by calculating Spearman's correlation coefficients. We used the same method to examine whether the monthly home range and core area sizes were affected by FAI. We adjusted for multiple comparisons using the Benjamini and Hochberg method (Benjamini & Hochberg, 1995), because it provides a better compromise between type I and type II errors than traditional Bonferroni methods (Nakagawa, 2004; Pike, 2011). This is more appropriate in our case due to small sample size ($n = 12$) (Jennions & Møller, 2003; Nakagawa, 2004). We also provided bootstrapped confidence intervals for every tested relationship to provide additional information about their biological relevance and statistical plausibility, as suggested by Nakagawa (2004).

To test our hypothesis that macaques are more effective seed dispersers for invasive than native plant species, we used a model selection approach based on the second-order Akaike information criterion (AICc). We first calculated the proportion of ripe vs unripe fruits consumed by macaques per feeding bout and used it as a measure for SDE. We fitted generalized linear models (GLMs) using the proportion of ripe vs unripe fruits consumed by macaques as response variable and 'Species' (consisting of all species macaques fed on) and monthly FAI as predictors. We fitted the GLMs with binomial error distributions, as our response variables were proportions derived from counts

(Douma & Weedon, 2019). Because we had an unequal number of samples in different months — during some months macaques did not feed on native fruit at all, and only three invasive species (*F. indica*, *Litsea* sp. and *P. cattleyanum*) made up nearly all of the ripe fruit macaques ate — we collapsed predictor ‘Species’ into two categories. The first category contained the three invasive species (referred to as ‘main invasive plants’) and the second contained the other plant species (referred to as ‘other’). We examined a set of models with all possible combinations of the explanatory variables, including a two-way interaction between the explanatory variables. We ranked the models based on AICc to find the most parsimonious models. We defined the most parsimonious models as those with a ΔAICc score ≤ 2 (Symonds & Moussalli, 2011). When models with a ΔAICc score ≤ 2 were more complex versions of the top-ranked model (with additional predictors or interactions), we eliminated them as recommended by Richards (2008) to avoid retaining overly complex models with potentially spurious covariates. We also ranked model weights for every predictor and two-way interactions, by summing the Akaike weights for each model in which that predictor or two-way interaction appeared. This weight is equivalent to the probability that that predictor is a component of the best model, with a summed weight close to 1 meaning that the predictor is highly likely to be part of the best model (Symonds & Moussalli, 2011). We used a similar model selection procedure to test the hypothesis that the probability of fruit rejection by macaques is affected by fruit maturity and availability, using GLMs with the proportion of fruits consumed vs dropped by macaques for both ripe and unripe fruits for every feeding bout as response variable and ‘Species’, monthly FAI, and ‘Fruit Maturity’ (ripe/unripe) as predictors. As we only include plausible predictors and interactions in our set of alternative models, our model selection procedure is appropriate for inference (Burnham *et al.*, 2011). In our case, model selection procedures also yield similar results to null-hypothesis significance testing (NHST) methods, due to the limited number of predictors (Castilho & Prado, 2021).

We assessed the fit of the most parsimonious models with residual diagnostic plots from package *DHARMA* (Hartig, 2021). Because the top-ranked models showed signs of under-dispersion, we refitted the models with quasi-binomial error distribution. Furthermore, the top-ranked model explaining variation in ripe vs unripe fruit consumption included a two-way interaction between ‘Species’ and monthly FAI and thus we calculated regression coefficients and *SEs* for the simple slopes of FAI for the two levels of ‘Species’ (using function *emmeans* from package *emmeans* – Lenth *et al.*, 2021). The top-ranked model explaining consumed vs dropped fruit also included a two-way interaction (between ‘Fruit Maturity’ and monthly FAI), and therefore we calculated pairwise comparisons between predicted marginal means of ‘Fruit Maturity’ levels (ripe/unripe) for low (mean FAI minus one *SD*), intermediate (mean FAI), and high (mean FAI plus one *SD*) FAI values.

Ethical Note

This research was non-invasive. The study conforms to the Code of Best Practices for Field Primatology for the Ethical Treatment of Non-Human Primates (International Primatological Society). Additionally, our research complied with the

conditions set by the National Parks and Conservation Service, Ministry of Agro Industry and Food Security (MOAFS) and was conducted under research permit No. RRRS1912359. The research was also approved by the Forestry Service, MOAFS in order to work on state land.

Data Availability The datasets collected and/or analysed during the current study are available from the corresponding author on reasonable request.

Results

Seasonality in Food Availability

We defined the high fruit availability period as February–June 2020, when monthly fruit availability index (FAI) scores were at least twice the *SE* (2110) above the mean (Fig. 2). The majority of stems along vegetation transects comprised invasive species (86%; Table S1) and invasive species accounted for the majority of the total FAI (70%) and FAI during the high fruit availability period (72%). Only three invasive species (*F. indica*, *Litsea* sp., and *P. cattleyanum*) accounted for the bulk of total FAI (63%; Table S1) and invasive FAI (90%). The native proportion of total FAI mostly comprised three native species (24% by *Canarium paniculatum*, *P. mauritianum*, and *S. glomeratum*; Table S1). Native species produced little fruit compared to invasives during our study period: only 15 out of 29 native species

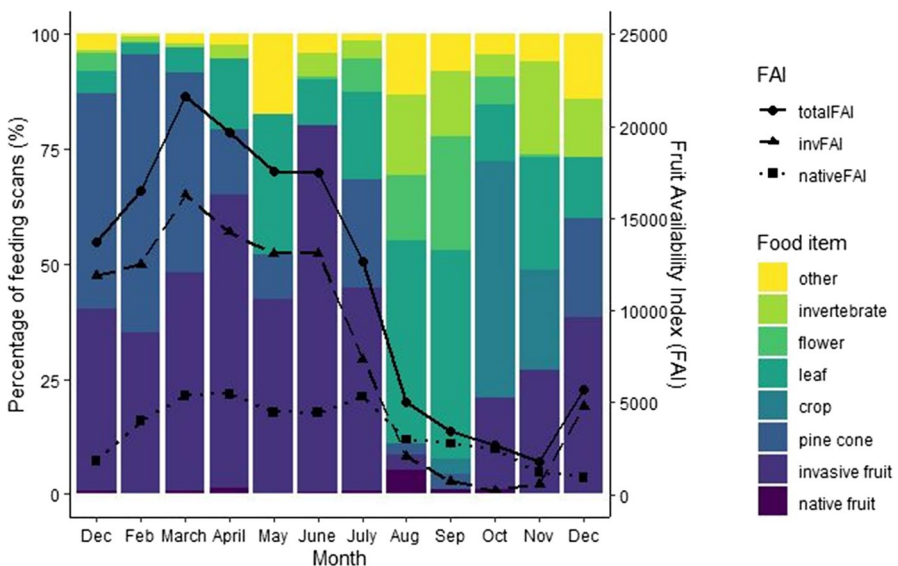


Fig. 2 Weighted monthly percentages of dietary scans long-tailed macaques (*Macaca fascicularis*) spent feeding on various food items (left y-axis) and the monthly fruit availability index (FAI) scores for all plant species (totalFAI), invasive plant species (invFAI), and native plant species (nativeFAI) in Mt. Calebasses (Mauritius) from December 2019 until December 2020.

produced fruits (only eight developed ripe fruits), whereas eight out of ten invasive species produced fruits during our study period (seven with ripe fruits; Table S1). Additionally, only 45% of native stems produced fruits, whereas 73% of invasive stems produced fruits (Table S1). Development of ripe fruit coincided with the high fruit availability period: out of all plant species that produced ripe fruits, 86% developed ripe fruits in the high fruit availability period (Table S1).

There was a clear peak and trough in FAI, due to the timing of fruiting of the disproportionately abundant *F. indica*, *Litsea* sp. and *P. cattleyanum*: *F. indica* fruited during the period December 2019–September 2020, *Litsea* sp. during December 2019–May 2020, and *P. cattleyanum* during December 2019–October 2020 (Table S1). Several native plant species remained available during the low fruit availability period (Table S1), but they contributed little to total FAI (~10%). Overall, native FAI was more stable than invasive FAI, showing a less clear peak than invasive FAI and a slower decline during the low fruit availability period (Fig. 2). The monthly flower availability index (FlAI) also showed a clear peak and trough during our study period (67 in June 2020 to 42,543 in October 2020). Invasive species also accounted for the majority of total FlAI (81%), mostly made up of only two species: *Litsea* sp. and *S. jambos* (93% of invasive FlAI). The pine cone availability index scores (PcAI) ranged from 20,655 in March 2020 to 9914 in August 2020, indicating that pine cone was a less variable resource compared to flowers and fruits.

Effects of Food Availability on Diet

The macaques spent the largest percentage of activity scans feeding (37%). The majority of these dietary scans was made up of fruit (40.4%), followed by pine cones (26.3%), leaves (15.5%), invertebrates (6.1%), flowers (4.1%), and crops (2.7%; Fig. 2). Pine cones were only consumed when unripe. Other food items included tree bark (0.5%), grasses (0.3%), and eggs (0.2%). A small proportion of the food items could not be identified during field observation due to poor visibility (3.9%). The percentage of dietary scans that macaques fed on fruit was strongly positively correlated with FAI (Table I; Fig. 2). We also found moderately strong negative correlations between FAI and the percentage of dietary scans that macaques fed on crops, flowers, and invertebrates (Table I), indicating that macaques increasingly fed on fruits as fruit became more abundant, whereas it increasingly fed on crops, flowers, and invertebrates as fruit became scarcer. We did not find statistically significant correlations between the percentages of time macaques fed on other food items and FAI, FlAI, and PcAI (Table I).

Macaques consumed plant parts of 36 plant species and the fruits of 17 plant species (Table S2). Feeding on invasive species comprised the majority of dietary scans when macaques fed on both all plant foods (98%) and fruit specifically (97%; Table S2). Of the dietary scans when macaques fed on fruit, the majority consisted of invasive *Litsea* sp. (40.2%) and *P. cattleyanum* (39.3%, Table S2), followed by invasive *F. indica* (9.5%), and non-native *Mangifera indica* (4.9%). Out of the small percentage of fruit feeding scans when macaques fed on native fruits (3%), *E. pyxidata* made up the largest percentage (24.1%), followed by *F. rubra* (20.7%) and *F.*

Table 1 Spearman correlation coefficients (rl) for the relationships between: (1) the monthly Fruit Availability Index (FAI) score and the weighted percentages of dietary scans long-tailed macaques (*Macaca fascicularis*) fed on different food items ($n = 12$ months), (2) the monthly Flower Availability Index (FlAI) score and the weighted percentages of dietary scans macaques fed on flowers ($n = 12$ months), (3) the monthly Pine cone Availability Index (PcAI) score and the weighted percentages of dietary scans macaques fed on pine cone ($n = 10$ months), and (4) invasive and native FAI and the weighted percentages of dietary scans macaques fed on invasive and native fruits ($n = 12$ months), from December 2019 until December 2020 in Mt. Calebasses, Mauritius

Relationship	rl	P _{raw}	P _{adjusted}	95% CI lower	95% CI upper
Fruit availability index (FAI)					
FAI — % fruit	0.81	< 0.01	0.03	0.64	0.98
FAI — % leaf	-0.41	0.19	0.23	-0.79	0.23
FAI — % flower	-0.69	0.01	0.04	-0.95	-0.19
FAI — % crop	-0.75	< 0.01	0.03	-0.90	-0.48
FAI — % invertebrate	-0.75	< 0.01	0.03	-0.96	-0.35
FAI — % pine cone	0.51	0.09	0.13	-0.20	0.89
Flower availability index (FlAI)					
FlAI — % flower	0.19	0.55	0.55	-0.48	0.67
Pine cone Availability Index (PcAI)					
PcAI — % pine cone	0.34	0.37	-	-0.50	0.85
Invasive/ native FAI					
Invasive FAI — % invasive fruit	0.82	< 0.01	< 0.01	0.63	0.98
Native FAI — % invasive fruit	0.64	0.03	0.06	0.16	0.94
Invasive FAI — % native fruit	0.09	0.78	0.78	-0.51	0.67
Native FAI — % native fruit	0.42	0.18	0.24	-0.18	0.85

Statistically significant coefficients are in bold letters

mauritiana (13.8%). The availability of invasive (invasive FAI) and native fruits (native FAI) peaked during the same period (February–July 2020) and invasive FAI was strongly positively correlated with the percentage of dietary scans when macaques fed on invasive fruits, whereas we did not find statistically significant correlations between invasive FAI and consumption of native fruit, or native FAI and consumption of invasive and native fruits (Table 1). The plant species with the highest fruit preference index (FPI_i) scores (> 1) were all invasive: *Litsea* sp. (4.0), *S. jambos* (1.2), and *P. cattleyanum* (1.1). All other plant species had FPI_i scores ≤ 0.8 (Table S2), indicating that macaques only preferred fruits of invasive plant species, especially *Litsea* sp., over other fruits during the period that they were available.

Effects of Fruit Availability on Home Range

Our study group had a total home range of 34.9 ha, mean monthly home range of $14.5 \pm \text{SD } 5.8$ ha (range: 6.3–28.4 ha) and mean monthly core area size of $3.2 \pm \text{SD } 1.7$ ha (range: 1.2–6.8 ha) (Fig. 3). During the high fruit availability period (February–June 2020), the mean monthly home range was $10.6 \pm \text{SD } 3.0$ ha and the mean

monthly core area size $2.2 \pm \text{SD } 0.7$ ha. Outside of the high fruit availability period, mean monthly home range was $17.8 \pm \text{SD } 5.6$ ha and the mean monthly core area size $3.95 \pm \text{SD } 2.0$ ha. Monthly home range and FAI were significantly negatively correlated ($|r| = -0.65$, $P_{\text{adjusted}} = 0.037$, CI low = -0.96 , CI up = -0.26), indicating that home range increased as fruit became less abundant. Core area size and FAI were negatively associated, but not statistically significant ($|r| = -0.41$, $P_{\text{adjusted}} = 0.21$, CI low = -0.85 , CI up = 0.15).

Seed Dispersal Effectiveness

We quantified fruit consumption and drop for a total of 114 feeding events (total feeding time = 14 hours) spread across 39 days from December 2019 until December 2020 (mean = $11 \pm \text{SD } 9$ events per month). The majority of fruits consumed and dropped by macaques were invasive (105 out of 114 total feeding events), and we mainly recorded consumption and drop of native fruits outside of the high fruit availability period (seven out of nine native fruit feeding events). Overall, macaques consumed more ripe than unripe fruits (61% ripe),

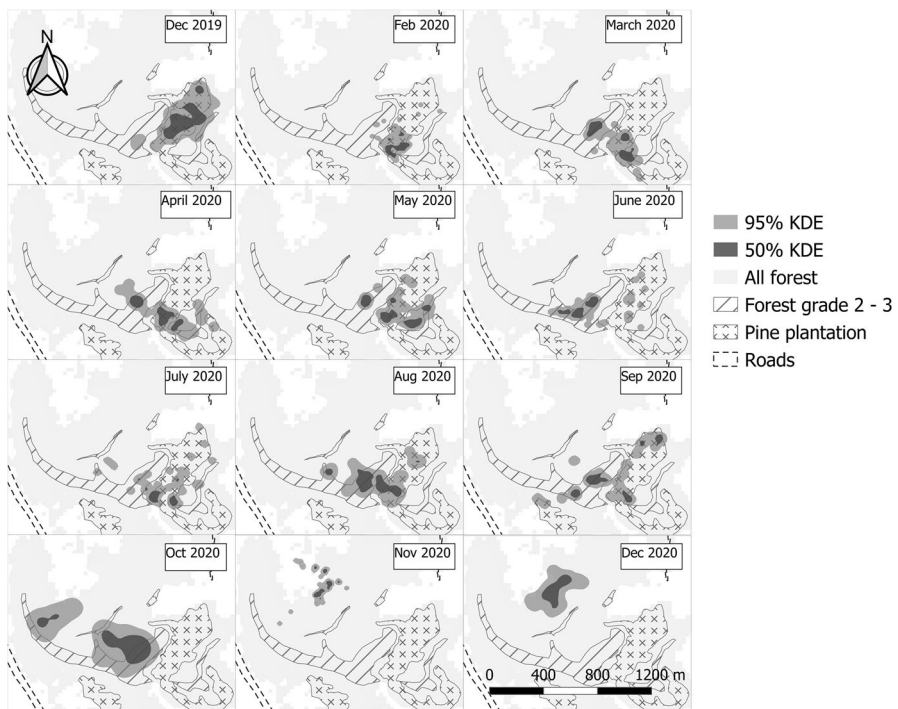


Fig. 3 Monthly home ranges of long-tailed macaques (*Macaca fascicularis*) in Mt. Calebasses (Mauritius) from December 2019 until December 2020, represented by the 95% kernel density estimate (KDE). Core areas are represented by the 50% KDE. Forest Grade 2–3 consists of at least $\geq 50\%$ but $\leq 75\%$ native plant cover.

but dropped less ripe than unripe fruits intact (20% ripe, Table II). Out of all the ripe fruits macaques handled, macaques consumed (94%) and dropped (73%) the majority during the high fruit availability period (February–June 2020). The percentages of ripe vs unripe fruits that macaques consumed were much smaller for native species (2%) than for invasive species (72%, Table II). Macaques consumed ripe fruits of only one native species (Table II). The percentages of ripe vs unripe fruits consumed by macaques were largest for invasive *F. indica* (95%), *P. cattleyanum* (84%) and *Litsea* sp. (74%). Combined, these three species made up 98% of ripe fruits consumed by macaques. Moreover, the most common types of fruit handling by macaques during the feeding events were: partly eating the fruit pulp and discarding the rest, plucking and dropping intact fruits, and destroying seeds (Table II). We only recorded seed spitting for invasive *Litsea* sp. (Table II), and we only observed seed destruction when fruits were unripe. Additionally, macaques consumed less fruit than it dropped overall (29%), but consumption vs drop varied greatly between species (mean = $50 \pm$ SD 31%, range = 0–100%; Table II). Fruit consumption vs drop by macaques was especially low for *Citrus* sp., *F. indica*, *F. reflexa*, *F. rubra*, and *Litsea* sp. (< 40%, Table II), indicating that the long-tailed macaque is a wasteful consumer for these species. For other species, macaques consumed large percentages of fruit, especially *E. pyxidata* and *F. mauritiana*, (> 75%, Table II).

The top-ranked GLM explaining the proportion of ripe vs unripe fruits consumed by macaques contained a two-way interaction between FAI and ‘Species’ (Δ AICc \leq 2, Table III), indicating a strong positive effect of FAI on the proportions of ripe vs unripe fruits of the main invasive species (*F. indica*, *Litsea* sp., and *P. cattleyanum*) consumed by macaques (Fig. 4; Table S3). The inclusion of the two-way interaction also indicated that FAI had a weak negative effect on the proportions of ripe vs unripe fruits of other plant species consumed by macaques, but the high SE relative to the regression coefficient indicated that this estimate was highly imprecise (Fig. 4; Table S3). The summed predictors weights for each predictor and interaction included in the top-ranked model were high (> 0.85; Table S4), indicating that it is highly likely these predictors are part of the best model. Therefore, our findings suggested macaques only increasingly consumed ripe fruits of *F. indica*, *Litsea* sp., and *P. cattleyanum*, and not for other plant species as fruit became more abundant.

The top-ranked model explaining the proportion of fruits consumed vs dropped by macaques included predictor ‘Species’ and a two-way interaction between FAI and ‘Fruit Maturity’. There were two more models with Δ AICc \leq 2, but these were more complex versions of the top-ranked model and thus we discarded them (Table III). The top-ranked model indicated that macaques dropped a significantly bigger proportion of fruit for *F. indica*, *Litsea* sp., and *P. cattleyanum* than other plant species (Fig. 4; Table S3) and that macaques dropped a higher proportion of unripe than ripe fruits during times of intermediate and high fruit availability and not during low fruit availability (Fig. 4; Table S3). The summed predictors weights for each predictor and interaction in the top-ranked model were high (> 0.95), whereas summed weights for interactions not included in the top-ranked model were

Table II Total ripe and unripe fruit eaten and dropped by long-tailed macaques (*Macaca fascicularis*) and median number of ripe and unripe fruits consumed and dropped per macaque per minute of the feeding bouts for different native and invasive plant species recorded during December 2019–December 2020 in Mt. Calabasses, Mauritius. The status, seed size (small = length < 5 mm, medium = length ≥ 5 mm but ≤ 10 mm, large = length > 10 mm), macaque fruit handling type (handling type), total number of sampled feeding bouts (*N*) and total feeding bout time in minutes (Time) are also given for every plant species.

Species	Status	Seed size	Handling type ¹	<i>N</i>	Time	Total fruit eaten		Total fruit dropped		Fruit/macaque/minute (median [<i>QR</i>])					
						Ripe	Unripe	Ripe	Unripe	Ripe eaten	Unripe eaten	Ripe drop	Unripe drop		
<i>Citrus</i> sp.	Invasive	Medium	Di/Dr	1	16	-	2	-	9	-	-	0.1	-	-	0.6
<i>Eugenia pyxidata</i>	Native	Large	De/Di/Dr	2	21	-	31	-	4	-	-	1.3[1.1–1.4]	-	-	0.1[0.04–0.1]
<i>Ficus mauritiana</i>	Native	Small	Di	2	13	-	19	-	-	-	-	3 [2.1–4]	-	-	-
<i>Ficus reflexa</i>	Native	Small	Di/Dr/Sw	2	13	-	-	-	11	21	-	-	-	0.6[0.3–0.8]	1.3[1–1.6]
<i>Ficus rubra</i>	Native	Small	Di/Dr/Sw	1	18	2	1	1	11	11	0.1	0.02	0.1	-	0.6
<i>Flacourtia indica</i>	Invasive	Small	Di/Dr	10	79	53	3	26	69	69	0.6[0.1–1.1]	0[0–0]	0.2[0–0.4]	0.7[0.1–1]	-
<i>Lisea</i> sp.	Invasive	Medium	Dr/Sp	33	272	142	50	222	769	769	0[0–0.7]	0[0–0.2]	0.2[0–1.1]	2[0.9–5]	-
<i>Mangifera indica</i>	Invasive ²	Large	De/Di/Dr	19	170	2	48	-	34	-	0[0–0]	0.3[0.1–0.5]	-	-	0.1[0–0.2]
<i>Noronha broomeana</i>	Native	Medium	De/Di/Dr	1	3	-	4	-	1	-	-	1.3	-	-	0.3
<i>Psidium cattleianum</i>	Invasive	Small	Di/Dr	40	218	168	33	35	20	20	0.7[0.3–1.2]	0[0–0.3]	0[0–0.2]	0[0–0.1]	-
<i>Syzgium dupontii</i>	Native	Medium	De/Di/Dr	1	8	-	5	-	4	-	-	0.6	-	-	0.5
<i>Syzgium jambos</i>	Invasive	Large	De/Di/Dr	2	11	-	2	-	4	-	-	0.8[0.4–1.1]	-	-	0.3[0.2–0.5]

¹De = seeds destroyed, Di = fruit partly eaten and discarded, Dr = fruit dropped intact, Sp = seed cleaned of pulp and spat out, Sw = fruit swallowed whole

²Non-native but not considered invasive in Mauritius

Table III AICc table of a priori models explaining effects of monthly fruit availability index (FAI) and ‘Species’ on the proportion of ripe vs unripe fruits consumed by long-tailed macaques (*Macaca fascicularis*) per feeding bout and the effects of ‘Fruit Maturity’, monthly FAI and ‘Species’ on the proportion fruits consumed vs dropped by macaques per feeding bout. We ranked models in ascending order of AICc. We collected the data used in the GLMs during December 2019–December 2020 in Mt. Calabasses, Mauritius.

Effects of FAI and Species on proportion ripe vs unripe fruit consumed	K	AICc	ΔAICc	W
Proportion ripe vs unripe ~ FAI * Species	4	115.9	0.0	0.869
Proportion ripe vs unripe ~ FAI + Species	3	120.7	4.7	0.081
Proportion ripe vs unripe ~ FAI	2	121.6	5.7	0.050
Proportion ripe vs unripe ~ 1	1	156.0	40.1	< 0.001
Effects of FAI, Fruit Maturity and Species on proportion consumed vs dropped fruit				
Proportion consumed vs dropped ~ Maturity * FAI + Species	5	153.9	0.0	0.5091
Proportion consumed vs dropped ~ Maturity * FAI + Species * FAI	6	155.1	1.2	0.2835
Proportion consumed vs dropped ~ Maturity * FAI + Species * Maturity	6	155.8	1.9	0.1990
Proportion consumed vs dropped ~ Maturity * Species + FAI	5	162.7	8.7	0.0065
Proportion consumed vs dropped ~ Maturity + Species + FAI	4	172.4	18.4	< 0.001
Proportion consumed vs dropped ~ Maturity + Species	3	179.0	25.0	< 0.001
Proportion consumed vs dropped ~ Maturity	2	194.1	40.2	< 0.001
Proportion consumed vs dropped ~ 1	1	207.8	53.9	< 0.001

low (< 0.5; Table S4). The regression coefficients and *SEs* for all predictors are summarized in Table S3.

Discussion

Seasonal Patterns in Diet Composition

Fruit was the most dominant component of our study group’s diet, similar to previous studies in Mauritius (Sussman *et al.*, 2011). Additionally, we found that macaques increasingly consumed ripe fruits as these became more abundant, contrary to flowers, invertebrates, crops, and unripe fruit, supporting our hypotheses. Therefore, our findings suggest long-tailed macaques in Mauritius have a similar dietary response to seasonal variation in fruit availability as their counterpart in South-East Asia (Lucas & Corlett, 1991; Ruslin *et al.*, 2019; Sha & Hanya, 2013; Yeager, 1996). Macaques probably preferred ripe fruits over unripe fruits, because both unripe and ripe fruits were available during high fruit availability. Macaques may also prefer ripe fruits over flowers and invertebrates: we did not find a relationship between flower consumption and flower availability, flowers were available during the high fruit availability period and we assume that invertebrates were available year-round. Therefore, flowers, unripe fruits, and invertebrates were probably ‘fallback’ foods for macaques during our study period.

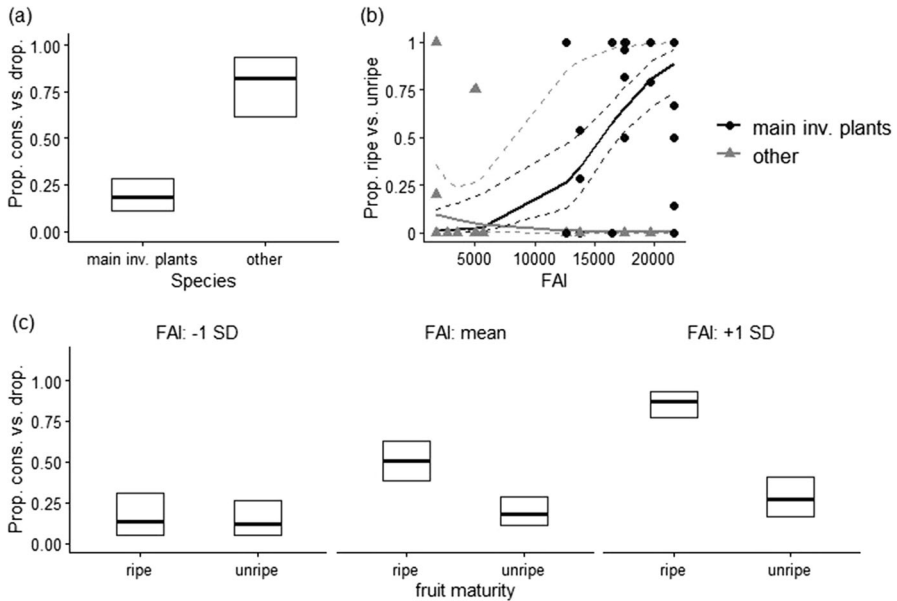


Fig. 4 **a** Predicted means and 95% confidence intervals for the proportion of fruits consumed (*cons.*) vs dropped (*drop.*) by long-tailed macaques (*Macaca fascicularis*) per feeding bout in relation to ‘Species’ (‘*main inv. plants*’ = invasive *Flacourtia indica*, *Litsea* sp., and *Psidium cattleianum*; ‘*other*’ = other native and invasive plant species) as estimated by the most parsimonious binomial generalized linear model (GLM) **b** Line of best fit with 95% confidence intervals (indicated by *dashed lines*) estimated by the most parsimonious binomial GLM expressing the relationship between monthly fruit availability index (FAI) scores and the proportion of ripe vs unripe fruits consumed by macaques per feeding bout for ‘*main inv. plants*’ and ‘*other*’. **c** Predicted marginal means and 95% confidence intervals for the proportion of fruits consumed vs dropped by macaques per feeding event in relation to ‘Fruit Maturity’ (ripe/unripe) for low (FAI: -1 SD), intermediate (FAI: mean) and high (FAI: $+1$ SD) FAI scores as estimated by the most parsimonious GLM. We collected the data used in these figures during December 2019–December 2020 in Mt. Calébasses, Mauritius.

After fruit, macaques spent most time feeding on unripe pine cones of *P. elliotii*, especially at the start of the high fruit availability period. One of the two birth peaks in Mauritian long-tailed macaques coincides with the high fruit availability period (March) (Jamieson, 1998). During pregnancy and lactation, female primates require a lot of protein (McCabe & Ferdigan, 2007), and unripe pine seeds are probably a better source of protein than ripe fruit pulp (White, 2011). Additionally, pine cones of *Pinus* spp. are high in condensed tannins (Eberhardt & Young, 1994), which females in some primate species increasingly consume during the birth season as a form of self-medication (Carrai *et al.*, 2003), because their immune system may be weakened due to increased allocation of protein to reproductive vs immune functions (Houdijk *et al.*, 2001). However, pine cones are also high in cellulose and should be more difficult to digest and thus less nutritious than fleshy fruit for macaques, because macaques

are hindgut-fermenters (Chivers, 1994). Nevertheless, unripe pine cones may be an important source of protein/tannins for macaque females, but additional research is required to confirm this, as we did not distinguish between males and females during feeding bouts.

Seasonal Ranging Patterns

Ranging patterns were also driven by fruit availability: home range increased as fruit availability decreased, aligning with our predictions. Most species that fruited during the low fruit availability period also occurred at low densities, probably forcing the macaques to range further. This increase in home range was also accompanied by a group migration to the orchards in October 2020. Ranging patterns and dietary patterns are often on an annual cycle for *Macaca* spp. (Hanya *et al.*, 2003), and macaque females are usually philopatric (Noordwijk & Van Schaik, 1999). Therefore, we consider the ranging behaviour in October 2020 a group migration or ‘expedition’ (Hanya *et al.*, 2002). From October until December 2020, the group spent most of its time feeding on mango (*M. indica*) on the forest edges and in the adjacent mango orchards. *Mangifera indica* was abundant near the forest edges that bordered the mango orchards, and very rare in the area that the group used prior to October 2020 (also not present on the vegetation transects). Therefore, the increase in home range enabled the group to access a new fruit source and maintain a relatively high proportion of fruit in their diet, despite low fruit availability within their original home range, indicating that macaques used energy-maximizing strategies.

The availability of commercial orchard fruits, such as mango (*M. indica*) and lychee (*Litchi chinensis*), may also have influenced patterns in diet composition and home range. Crops were increasingly consumed as forest fruit became less abundant, and the start of the fruiting season of the main orchard fruits (*M. indica* and *L. chinensis*) coincides with the end of the low fruit availability period (September–October). Anthropogenic foods, such as crops, may offer energetic/nutritional advantages to primates compared to wild fruits (Riley *et al.*, 2013; Strum, 2010), and the accessibility of these foods typically influences foraging patterns of primates (Cancelliere *et al.* 2018), including *Macaca* spp. (Gazagne, José-Domínguez, *et al.*, 2020b; Sha & Hanya, 2013b).

The ongoing capture of macaques at the forest edges near the orchards may be another important factor that can explain the observed ranging patterns. Macaques in Mauritius are captured year-round by various local monkey breeders that export the animals for medical research and by locals that are encouraged to capture and sell macaques to the monkey breeders. We were informed by orchard farmers from Vallée du Paradis that macaques were captured year-round in this area. We confirmed this, because we found several cage traps with minor rust stains near the new sleeping site of our group. As far as we are aware, nobody carried out capture/trapping activities when our group moved into this area, but capture by humans may have potentially dissolved a group that occupied the area before our group (Sugiyama & Ohsawa, 1982). This may have provided our study

group with an opportunity to range outside of their original home range in October 2020. For example, food scarcity, macaque capture by humans, and/or lack of adjacent groups often drive group migrations in Japanese macaques (*Macaca fuscata*) that occupy habitat heavily modified by humans (Hanya *et al.*, 2002; Sugiyama & Ohsawa, 1982).

Foraging Strategies and Seed Dispersal Effectiveness

Macaques predominantly fed on the fruits of three invasive species (*F. indica*, *Litsea* sp., and *P. cattleyanum*, all highly invasive) and increasingly fed on ripe vs unripe fruits of these species as fruit became more abundant. These three invasive species also made up nearly all ripe fruit consumed by macaques, agreeing with our prediction that macaques mainly feeds on ripe invasive vs native fruits. In contrast, the vast majority of native fruits consumed by macaques were unripe, aligning with previous studies (Baider & Florens, 2006; Krivek, 2017; Reinegger *et al.*, 2021). Four native species (*E. pyxidata*, *F. mauritiana*, *N. broomeana*, *S. dupontii*) were even exclusively consumed when unripe. Even though in some cases fruit does not have to be ripe in order for seeds to germinate (Cruz-Tejada *et al.*, 2018), generally ripeness of a fruit is an indicator for seed germination success (Sumner & Mollon, 2000). Therefore, our findings indicate macaques may potentially be a poor seed disperser for many native plants and a major seed disperser for three of the most invasive woody plants in Mauritius: *F. indica*, *Litsea* sp., and *P. cattleyanum*.

We also found differences in fruit-handling behaviour between native and invasive plants, indicating additional differences in SDE between invasive and native plants. We only recorded seed spitting for invasive *Litsea* sp., which is considered an effective seed dispersal mechanism (Gross-Camp & Kaplin, 2011), and we often found mature seeds of invasive *F. indica* and *P. cattleyanum* in the faeces of macaques (RR pers. obs.). In contrast, macaques typically destroyed the soft seeds within unripe native fruits, indicating that macaques may mostly act as seed predator instead of seed disperser for native species. However, as macaques consumed most native species during the low fruit availability period when home ranges were larger, there is potential for higher SDE, as the frequency of long-distance dispersal events may be higher (Chapman & Russo, 2006). Nevertheless, the negative effects of exclusive consumption of unripe fruit and/or seed predation may largely outweigh the benefits of larger dispersal distances for the plants consumed.

The macaques probably further enhance differences in SDE between invasive and native plants by discarding more fruit when foraging on unripe fruit. In line with our predictions, macaques rejected more unripe than ripe fruit when fruit was abundant. Conversely, during low fruit availability, there was no difference in rejection by macaques between ripe and unripe fruit. According to optimal foraging theory, primates are expected to increasingly reject fruits of lower quality when the chances of obtaining higher quality fruits increase during high fruit availability, and may thus become increasingly 'choosy' (Janson, 1996). Consequently, (unripe) native fruits handled by macaques have a high chance of being rejected, probably leading to

dispersal failure. However, we also found that macaques rejected significantly more fruit of *F. indica*, *Litsea* sp., and *P. cattleyanum* (especially *F. indica* and *Litsea* sp.) than other species, presumably because these species have the largest fruit crops out of all the species macaques ate, giving the macaques more fruit to choose from. Nevertheless, unlike native species, macaques compensate for wasted fruit of these invasive species by consuming more ripe fruit when fruit availability is high, and seed dispersal limitation is probably also largely avoided due to large fruit crops.

Factors Explaining Observed Foraging Strategies and SDE

The general preference for invasive fruits can partly explain the observed foraging patterns of macaques and the resulting differences in SDE between native and invasive plants: macaques disproportionately selected three invasive plant species relative to their availability (S_i – scores > 1: *Litsea* sp., *S. jambos*, and *P. cattleyanum*), suggesting that these species were preferred. The availability of *Litsea* sp. may be particularly important in explaining foraging patterns of the macaques, because its preference index score was nearly 4 times higher than the other two preferred species.

Morphological traits may partly explain preference for these fruits. All three preferred species have juicy pulp and external covers that are not difficult to pierce: traits preferred by some *Macaca* spp. (Sengupta & Radhakrishna, 2015). However, non-preferred native species that fruited simultaneously also possess these traits (e.g., *E. pyxidata* and *P. mauritianum*). Only *P. cattleyanum* appears to really stand out from the native fruits in our study site morphologically: the ripe fruits are very sweet, slightly acidic, and bright red/yellow. The long-tailed macaque is known to prefer juicy, acidic, and sweet fruits (Ungar, 1995) and primates are known to select bright yellow, orange, and sometimes red colours (Gautier-Hion *et al.*, 1985; Skalníková *et al.*, 2020; Terborgh, 1983), attributed to their trichromatic vision (Mollon, 1991). *Litsea* sp. and *S. jambos* do not possess these traits, but the long-tailed macaque also consumes *L. glutinosa* in its native range (Azzahra, 2017), and *Macaca* spp. generally prefer food plants in the genera *Litsea* and *Syzygium* (Sengupta *et al.*, 2020). Fruit nutrient and energy content analysis may provide insights into why these species are preferred over native fruits by long-tailed macaques in Mauritius. For example, the high lipid, protein, and energy content of invasive plants (including *Litsea* sp.) largely explains the preference of native frugivores for invasive over native fruits in the Seychelles (Kueffer *et al.*, 2009), preference for invasive over native fruits by frugivores in California (Vilá & D'Antonio, 1998), and the attractiveness of cultivated cacao to Tonkean macaques (*Macaca tonkeana*) in Indonesia (Riley *et al.*, 2013).

Imbalance in availability between invasive and native fruits may be another important factor in explaining the observed differences in consumption of ripe vs unripe invasive and native fruits. The fruiting success of the relatively few invasive species in our study area was greater than of the much greater number of native species. Invasive species also occurred at much higher densities than native species. Only three invasive species (*F. indica*, *Litsea* sp. and *P. cattleyanum*) accounted for the bulk of all fruit combined, and there was high overlap between their fruiting

periods, resulting in a clear peak and trough in fruit availability. Even though the fruits of several native species remained available during the low fruit availability period, they were scarce and contributed little to total FAI. Development of ripe fruit of most species coincided with the high fruit availability period (February–June 2020), and macaques consumed the vast majority of ripe fruit during the high fruit availability period as a result. Macaques mostly consumed native fruits outside of the high fruit availability period, partly explaining why macaques consumed these almost exclusively when unripe. Nevertheless, the high preference index score of some invasive species, especially *Litsea* sp., indicates that macaques may disproportionately feed on the ripe fruits of these species regardless of high relative abundance compared to native species.

To some extent, the adaptations of many large-seeded native canopy trees to seed dispersal by fruit bats (e.g., *Pteropus niger*) may also explain the consumption of primarily unripe native fruits. The ripe fruits of these trees predominantly have inconspicuous colours (green/ brown) and strong odours (Nyhagen, 2004). Just like other primates, the long-tailed macaque probably depends on its trichromatic vision to detect and select ripe fruits (Onstein *et al.*, 2020; Skalníková *et al.* 2020), which is not useful when ripe fruits remains brown or green. Primates also use olfactory cues to detect ripe fruit (Nevo & Valenta, 2018), but their sense of smell may be less developed than that of fruit bats (e.g., more suitable for short distances) (Nevo & Heymann, 2015). Additionally, the odour of ripe native fruits in Mauritius may be less recognizable for macaques than they are for the endemic fruit bats, as the specific bouquet of volatile organic compounds (VOCs) emitted by fruits to signal ripeness can vary geographically and between plants that rely on different seed disperser guilds (Nevo & Valenta, 2018). Therefore, the long-tailed macaque may have difficulty selecting ripe native fruits in Mauritius.

Implications for Conservation and Future Directions

The contrasting SDE of macaques for invasive and native plant species as a result of their foraging strategies may promote plant invasion: regeneration of invasive plants may be enhanced, whereas regeneration of native plants may be halted. Additionally, waste and consumption of unripe native fruits may further halt native plant regeneration by making fruit unavailable to endemic seed dispersers that mostly consume ripe native fruits, such as the endemic bat *P. niger* (Reinegger *et al.*, 2021). We argue the macaques have similar impacts elsewhere on the island, because the imbalance in fruit production is a common phenomenon across all remnant forests. Invasive plants, such as *F. indica*, *Litsea* sp., and *P. cattleyanum*, dominate native remnant forests across the island (Florens *et al.*, 2016; Florens *et al.*, 2017; Strahm, 1993), where they inhibit growth (Florens, 2008) and flower/fruit production of native trees (Krivek *et al.*, 2020; Monty *et al.*, 2013).

To confirm that foraging strategies of the macaques promote plant invasion, it is necessary to assess all aspects of SDE. Ideally, SDE is measured as the number of new adult plants produced by dispersal activities of an animal (Schupp *et al.*, 2010).

To confirm that the observed patterns in fruit consumption lead to disproportional recruitment of invasive plants, it would be necessary to also quantify seeds dispersed through faeces and carry out seed germination/seedling recruitment experiments. Moreover, it would be valuable to monitor seedling recruitment before and after macaque exclusion to better understand SDE of macaques and how macaques induce changes in vegetation composition. Complete exclusion is not realistic on a large scale, but local control of macaques in isolated forest fragments that are poorly connected to other forest patches may be feasible with assistance from local monkey breeding companies.

To better understand the potential contribution of the macaques to plant invasion at an island scale, it is necessary to conduct a population census. The last census was conducted in the 1980s and it is currently unknown how large the macaque population is or how densities vary between habitats and regions. Population growth has probably been limited by capture and export to some extent (Sussman *et al.*, 2011), but the population may still be as large as 40,000 individuals or higher (Bertram, 1994). Reports of macaques moving into urban areas and harassing residents have become common (L'Express, 2017, 2020a, 2020b), suggesting that insufficient suitable forest habitat is available. Therefore, it is essential to estimate the population size to develop a deeper understanding of the magnitude of the potential impacts of macaques on plant communities at an island scale. Nevertheless, our study was an essential first step in understanding the effects of the macaques on native plant communities.

Conclusion

Here, we presented an example of how foraging patterns of an invasive primate may promote plant invasion, due to imbalance in availability between invasive and native fruits and general preference for invasive fruits. Our example may be uncommon among invasive macaques and other invasive primates, because there are few regions with invasive primates where plant invasion has progressed to the point where invasive plants have largely replaced native plants (e.g., Angaur; Kemp & Burnett, 2003). However, the growing anthropogenic pressure on insular habitats (Kueffer & Kinney, 2017) and the resulting continued spread of invasive plants (Seebens *et al.*, 2015) may increase the potential for negative impacts of invasive primates on islands. Therefore, similar differences in SDE of invasive primates between native and invasive plants may be expected on islands elsewhere. Nevertheless, there are still only a few examples of impacts of invasive primates as seed dispersers, and further research is required to make valid generalizations.

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Author Contributions RDR and RZO formulated the idea. RDR designed the study, collected and analysed the data. GJ, RZO and EG reviewed methodology/data analyses and provided editorial advice. RDR wrote the manuscript with input from GJ, RZO, and EG.

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Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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