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Seed Shadows of Northern Pigtailed Macaques within a Degraded Forest Fragment, Thailand

Eva Gazagne ^{1,2,*}, Jean-Luc Pitance ¹, Tommaso Savini ², Marie-Claude Huynen ¹, Pascal Poncin ³, Fany Brotcorne ¹  and Alain Hambuckers ¹ 

¹ Research Unit SPHERES, Behavioural Biology Lab, Department of Biology, Ecology, and Evolution, Faculty of Sciences, University of Liège, Quai van Beneden, 22, 4020 Liège, Belgium; jl@pitance.eu (J.-L.P.); taude.huynen@gmail.com (M.-C.H.); fbrotcorne@gmail.com (F.B.); alain.hambuckers@uliege.be (A.H.)

² Conservation Ecology Program, Department of Natural Resources Management, School of Bioresources and Technology, King Mongkut's University of Technology Thonburi, 49 Soi Tienthalay 25, Bangkhuntien-Chaithalay Road, Thakham, Bangkhuntien, Bangkok 10150, Thailand; tommasosavini@gmail.com

³ Research Unit FOCUS, Behavioural Biology Lab, Department of Biology, Ecology, and Evolution, Faculty of Sciences, University of Liège, Quai van Beneden 22, 4020 Liège, Belgium; P.Poncin@uliege.be

* Correspondence: Eva.gazagne@alumni.uliege.be

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Abstract: Research Highlights: Frugivores able to disperse large seeds over large distances are indispensable for seedling recruitment, colonization and regeneration of tropical forests. Understanding their effectiveness as seed dispersal agents in degraded habitat is becoming a pressing issue because of escalating anthropogenic disturbance. Although of paramount importance in the matter, animal behaviour's influence on seed shadows (i.e., seed deposition pattern of a plant population) is difficult to evaluate by direct observations. Background and Objectives: We illustrated a modeling approach of seed shadows incorporating field-collected data on a troop of northern pigtailed macaques (*Macaca leonina*) inhabiting a degraded forest fragment in Thailand, by implementing a mechanistic model of seed deposition with random components. Materials and Methods: We parameterized the mechanistic model of seed deposition with macaque feeding behavior (i.e., consumed fruit species, seed treatments), gut and cheek pouch retention time, location of feeding and sleeping sites, monthly photoperiod and movement patterns based on monthly native fruit availability using Hidden Markov models (HMM). Results: We found that northern pigtailed macaques dispersed at least 5.5% of the seeds into plantation forests, with a majority of medium- to large-seeded species across large distances (mean > 500 m, maximum range of 2300 m), promoting genetic mixing and colonization of plantation forests. Additionally, the macaques produced complementary seed shadows, with a sparse distribution of seeds spat out locally (mean >50 m, maximum range of 870 m) that probably ensures seedling recruitment of the immediate plant populations. Conclusions: Macaques' large dispersal distance reliability is often underestimated and overlooked; however, their behavioral flexibility places them among the last remaining dispersers of large seeds in disturbed habitats. Our study shows that this taxon is likely to maintain significant seed dispersal services and promote forest regeneration in degraded forest fragments.

Keywords: large seeds; seed shadows; retention time; *Macaca leonina*; forest regeneration

1. Introduction

Anthropogenic disturbance is so prevalent that no pristine ecosystem remains across the world. Primary tropical forest loss and degradation due to agriculture, plantations and infrastructural conversions, are the driving forces of a massive tropical biodiversity crisis [1,2]. Seed dispersal

or the movement of seeds away from their parent plant, not only influences spatial structure and dynamics of plant populations, ensuring forest recruitment and regeneration but also allows establishing linkages between degraded habitats [3–5]. Dispersal away from the parent plant reduces density-dependent and distance-dependent seed and seedling mortality, while favoring gene flow and dispersal towards a suitable site for germination and establishment [6–8]. Typically, long-distance dispersal, although infrequent, allows connection between fragmented populations and colonization of new and degraded habitats [9]. Therefore, determining the seed deposition pattern of a plant population, its seed shadow [3] in degraded habitats, is crucial for providing the template for the spatial distribution of adult plants, understanding dispersal processes within particular habitats including the outcomes of the post dispersal processes [10] and predicting the evolution of forest ecosystems [11,12].

Habitat loss, fragmentation and degradation hamper seed dispersal [13]. As habitats shrink and disconnect, limited movements of frugivorous communities reduce seed dispersal distances and in turn disturb forests' structure, composition, ultimately threatening overall tropical biodiversity [1,2,5]. Modifying plant species richness and abundance affects fruit biomass production [14], as well as functional diversity and quality of fruits [15]. Consequently, habitat degradation alters both resource availability and quality for frugivores remaining in disturbed habitats, directly influencing their survival [16]. Medium to large body frugivores are especially vulnerable to habitat disturbance and the related increased hunting pressure. Their extirpation can drastically impede dispersal of large seeds which could not be dispersed by smaller frugivores [6,9,17]. For instance, in Asian degraded habitats, the major dispersers of large seeds and large-seeded fruits (e.g., elephants, rhinoceroses, gaurs, bears, tapirs, deer, large fruit bats, gibbons and hornbills), have either disappeared or reduced and are often threatened with extinction [14,18,19]. The few medium frugivores left, such as macaques, pigeons, bulbuls and civets, tolerate these disturbances and potentially ensure long-distance dispersion of relatively large-seeded fruits [19,20]. Studying frugivores able to disperse large seeds over large distances in degraded habitats therefore becomes a pressing issue for habitat restoration as well as for conservation of frugivores' communities themselves.

In Southeast Asia, frugivore primates are known as efficient dispersers of a high variety of large-seeded trees and lianas, playing a crucial role in maintaining species diversity in tropical forests [19,21–23]. Among primates, medium-bodied cercopithecine species are potentially the most effective seed dispersers in degraded habitats because of their diversified fruit diets, semi-terrestrial habits, large home ranges and ecological flexibility [24–26]. Since several species can adapt to various habitat conditions, such as those associated with heavy human disturbance and degradation, cercopithecine species are often the last large seed dispersers left in degraded forest fragments [24]. Additionally, they can provide complementary dispersal services for the same fruit species, via sparse dispersion of seeds of fruits kept in their cheek pouches (before processing them and spitting out the seeds) and longer dispersal distances of swallowed seeds due to long gut retention times and important travel distances [23,27]. In a study conducted in Khao Yai National Park, Albert et al. [28] demonstrated that Northern pigtailed macaques (*Macaca leonina*) are effective seed dispersers in both quantitative and qualitative terms (sensus Schupp et al. [8]); they disperse many seeds of many sizes and species into various natural habitat types, through various seed-processing methods (i.e., swallowing, spitting and dropping) and their effect on seed germination and viability remains neutral for most species. However, the authors could not define seed shadow since neither the gut retention time of the swallowed seeds nor their dispersal distances were known.

Determining seed shadow generated by frugivores is difficult and requires considerable information. In fact, a realistic description of plant seed shadows needs to take into account seasonal resource availability, plant traits, as well as the disperser morphology, physiology, movement and behavior [12,29–31]. The main objective of this study is to illustrate a modeling approach of simulated seed shadows which incorporates field-collected data and account for primates' movement patterns, feeding behavior and seasonal variations of resources. To this end, we collected information on a troop of northern pigtailed macaques in a degraded habitat at the Sakaerat Biosphere Reserve

(Sakaerat hereafter), North-Eastern Thailand. The troop was highly frugivorous with a large home range and long daily travels, covering natural dry-evergreen forest and old growth plantations [32]. We aimed to evaluate the macaques' general spatial pattern of dispersed seeds (i.e., the sum of seed shadows for all dispersed fruit species) in a degraded habitat and test whether or not macaques would disperse seeds within degraded areas and bring native, large-seeded species into reclaimed plantation forests. We hypothesized that due to their large ranging pattern and their flexibility in multi-habitat use, macaque could effectively disperse large seeds, over large distances and from native to plantation forests. To test this hypothesis, we first recorded macaques' movement pattern, daily activity, sleeping and feeding site location, fruit species consumption, as well as seed processing and deposition. Second, we analyzed the movement in the monthly home ranges in relation to native forest fruit availability using a Hidden Markov Model (HMM) as it allows us to capture the seasonal variations in macaques' movement patterns. Third, we adapted and ran a mechanistic model of seed deposition with random components [33] combining HMM results, monthly resource availability (i.e., sleeping and feeding sites), gut and cheek pouch retention times, which then simulated seed deposition patterns in the macaques' home range.

2. Materials and Methods

2.1. Study Site

We conducted the study in the degraded Sakaerat Biosphere Reserve (14°26' to 14°32' N; 101°50' to 101°57' E), North-Eastern Thailand. The core area of this reserve covers 80 km², with altitude ranging between 250 and 762 m above sea level. The climate is monsoonal, with a wet season (from May to October) and a relatively dry season divided into a cool (from November to February) and a hot (from March to April) periods. Mean annual temperature is 25.6 °C, while mean annual rainfall in the region is of 1200 mm [34]. Sakaerat has undergone severe deforestation and forest conversion, from pristine Dry-Evergreen Forest (DEF) to plantation forests (dominated by *Acacia mangium* and *Eucalyptus camaldulensis*). Currently, the reserve is covered by a mosaic of DEF (53.4%), Dry-Dipterocarp Forest (DDF) (14.8%), old-growth plantation forest (21.4%), grassland (6.1%), agroforestry (2.6%), bamboo patches (1.5%) and human settlements (0.2%) with an adjoining 5-lane highway and has reduced natural resource availability [32,35]. Finally, along with common barking deer (*Muntiacus muntjak*), common palm civet (*Paradoxurus hermaphrodites*), wild boar (*Sus scrofa*) and pigeons (*Columbidae*), northern pigtailed macaques are part of the remaining dispersers for large seeds left in Sakaerat [36]. Elephants and gibbons have been locally extinct for more than fifty years (T. Artchawakom, pers. comm.), while Asiatic black bear (*Ursus thibetanus*) and Oriental pied hornbill (*Anhracoceros albirostris*), which could potentially complete the dispersal network of large-seeded species, occur at very low densities [37,38].

2.2. Study Troop

We studied a wild troop of northern pigtailed macaques over three study periods across 12 months (April–July 2017, November 2017–March 2018 and August–October 2018). Troop size ranged from 123 to 153 individuals (mean of 141 ± SD 10 individuals), with 11–15 adult males, 41–48 adult females, 9–13 sub-adult males, 55–60 juveniles and 9–23 infants.

2.3. Data Collection

We followed the Sakaerat troop during 83 full days, from sleeping site to sleeping site (ca. 6 a.m. to 6 p.m.), with an average of 6.9 ± SD 0.5 days per month (range: 6–8 days). We recorded macaques' location using track-log data at 15-min interval with a handheld Global Positioning System (GPSmap 62 s, Garmin; Olathe, USA; ≤10 m error) and we used the Universal Transverse Mercator (UTM) format projection (zone 47N). We also recorded the location and time at which the troop entered and exited the sleeping site. Since the studied troop spread across several trees while sleeping, we placed the

sleeping site at the estimated center of the observed sleeping trees, based on the macaques' location in the evening and the next morning. We defined sleeping site as the circular area of a 75 m radius from the estimated center [39]. A previous study of Gazagne et al. [39] showed that the studied troop of northern pigtailed macaques selected a high number of sleeping sites with very few sites reused, following low availability and scattered distribution of fruit resources within Sakaerat.

To estimate the dispersed seed species and treatments, we used 30-min interval scan sampling, coupled with ad libitum sampling [40] to record the macaques' feeding behavior: consumed species, fruit parts eaten (seeds, pulp or whole fruit) and processing methods (swallow, spit out, drop, crunch). Additionally, as the troop rather spread out while feeding and sometimes split into two or three subgroups [39], we defined important feeding site (collected ad libitum) as the circular area of a 25 m radius from the estimated center of the subgroups and where the troop fed simultaneously for more than 10 min. The 25 m radius is based on the estimated mean spread of the study troop at the important feeding site (i.e., ~50 m) obtained with a GPS by walking along two perpendicular diameters at the estimated center. For each important feeding site, we collected the consumed fruit species, the fruit parts eaten and processing methods used. Probability of monthly important feeding site reuse by the study troop was 0.08 (ranging from 0 to 0.23; E. Gazagne, unpublished data). Finally, we collected fecal samples ad libitum, estimated the number of feces containing seeds, quantity of seeds in each fecal sample, seed species and seed size.

2.4. Fruit Availability

To estimate the density of tree species in Sakaerat, we mapped all individual tree trunks (i.e., stems) with diameter at breast height ≥ 10 cm along 15 botanical transects (100-m long and 20-m wide), covering 3 ha of DEF and 1 ha of plantation forests. We estimated the overall fruit availability along 12 phenological transects (within the troop home range) by recording monthly phenology of 10 individual trees for $N = 41$ fruit species (included in the troop diet). We quantified the fruit in the crown using a 5-point scale: 0 = no fruit; 1 = 1%–25%; 2 = 26%–50%; 3 = 51%–75%; and 4 = 76%–100%. To analyze the monthly variation in food availability in each forest type, we used a Fruit Availability Index (FAI) for each month (m) [32]:

$$FAI_m = \sum_{k=1}^n D_k B_k P_{km} \quad (1)$$

where D is the density of a given species k (stems/ha), B is the mean basal area of the trees of each k species (cm^2/ha) and P is the mean fruit phenology score of a given species within the corresponding month.

2.5. Ranging and Movement Patterns

We calculated monthly home ranges using a 100% Minimum Convex Polygon (MCP) and subtracted areas that we were confident the troop had never used during the study (i.e., dry-dipterocarp forest, human settlements and highway). We analyzed macaques' trajectories obtained from consecutive full tracking days (15-min track locations) using a Hidden Markov Model (HMM) with the R package `moveHMM` [41]. The HMM method uses predefined parameter values controlled by an unobservable Markov chain [42] to detect trends in time series tracking data (i.e., step length and turning angle variations) and compute probabilities of switching between spatial movement patterns, defined as behavioral states [43,44]. The models can be incorporated with environmental factors that may influence the probabilities of behavioral states. We used a zero-inflated gamma distribution for track step lengths (in meters) and a von Mises distribution for turning angles (in radians) of the macaques' trajectories to run HMM. We considered a three-state model interpreted as follows: (1) «foraging/resting» which corresponds to a slow and variable movement; (2) «foraging/transiting» which corresponds to a faster but variable movement; and (3) «transiting» which corresponds to a fast and directed movement.

Gazagne et al. [32] previously demonstrated that the model transition probabilities were a function of FAI in the DEF.

2.6. *In Situ Retention Times and Dispersal Distances*

We estimated macaque gut retention time by combining both feeding and defecation data. When identifiable individuals were feeding on a new fruit resource, we recorded ad libitum the time of feeding (mid-point of the feeding episode), species and location of the feeding site [45]. In the following days, every fecal sample of the same individual was examined until we found a seed belonging to the recorded species. We recorded the time of rejection and location of the rejected seed. Because we could not control the effect of foraging prior to our observations, gut retention times were not estimated for seeds defecated in the first two days of the data collection periods [46]. We discarded from the gut retention estimation all defecated seeds of which we were unable to determine the defecation time (e.g., found at the sleeping site) [30]. We used the same technique to estimate the cheek pouch retention times by recording the time of storing seeds and location of feeding tree. Thereafter, we followed the identifiable individuals and recorded the time and position of spat out seeds if they were to leave the crown radius of the feeding tree. As it was not possible to conduct continuous focal animal sampling [40] for a predetermined period in this large troop when at feeding sites (because of low visibility due to dense vegetation and constant turnover of individuals at feeding trees), we only recorded cheek pouch retention time on individuals that left their feeding trees immediately after storing the seeds (i.e., individuals were easier to observe while travelling).

Following the criterion used in Heymann et al. [47], we estimated the dispersal distances by recording the GPS coordinates of each feeding plant and of dispersed seeds (defecated or spat out). In other words, dispersal distances were a function of the time macaques retained seeds and their displacement distance during that time [45]. However, if macaques fed on several plants of the same species, the dispersal distance for swallowed or spat out seeds could not be determined.

2.7. *Mechanistic Model of Seed Transfer (MOST) and Data Analysis*

We adapted the code in FORTRAN 90 of the mechanistic Model of Seed Transfer (MOST) from Raghunathan [33] (Figure 1) by combining 3-state HMM outputs for movement characteristics accounting for seasonal variations in fruit availability, feeding and sleeping site locations, known gut and cheek pouch retention times, macaque feeding behavior (i.e., monthly fruit species consumption, seed treatments) and daily activity variations per month (data available online: <https://github.com/biocomp-most/most>). Movement simulations used HMM parameters for each behavioral state (steps-lengths and turning angles) and transition probability between states, varying with monthly fruit availability. The model also includes random components for retention times and macaque daily activity in order to account for natural variation. This code used Fortran library for cumulative density functions (CDFLIB) to calculate all statistical functions, that is, reverse gamma, reverse Von Mises' and reverse Gaussian [48] and is available in <https://github.com/biocomp-most/most/releases/tag/v1.0>.

The model starts by reading coordinates of monthly home ranges (100% MCP) and of monthly sleeping site and feeding site positions. To simulate macaque daily path length, we considered a succession of a mean of $49 \pm \text{SD } 2$ steps (range: 45–53; successive positions separated by 15 min), corresponding to an average of $11 \text{ h } 50 \pm \text{SD } 29$ min daily activity outside sleeping sites. Since diurnal length varies according to season, the procedure simulated the beginning and the end of the day by generating stochastic values within a Gaussian distribution based on macaques' mean time ($\pm \text{SD}$) of entering and leaving sleeping sites according to months (Table A1). The initial sleeping site among available monthly sleeping sites varied for each monthly simulation. To generate the first step and the first angle to reach the first position from the initial sleeping site, we initiated the simulation by setting the initial state of the HMM to the "foraging/resting" state. For each of the generated steps, the model verified that the position was located within the 100% monthly MCP using the "Winding Number" algorithm [49]; if not, new values of step and angle were redrawn. We recorded

the characteristics and behavioral state of the reached position and repeated the process. To simulate the end of the day, 30 min before macaques entered a sleeping site (i.e., 3 steps before macaques' day end), we oriented the drawn angles toward the nearest sleeping site, while the last step generated the next selected position. Since the macaque troop reused their sleeping sites at random [39], we gave an equal reuse-frequency for each sleeping site. Macaques could possibly enter sooner in a sleeping site if the calculated position within the last 30 min was located in the 75 m radius of a sleeping site. If no sleeping sites were encountered during that time, the program searched the sleeping site closest to the last point. The selected sleeping site at the end of the day corresponded to the departure site on the next morning. We performed 100 simulations per month with each run of the model that simulated seven consecutive days per month.

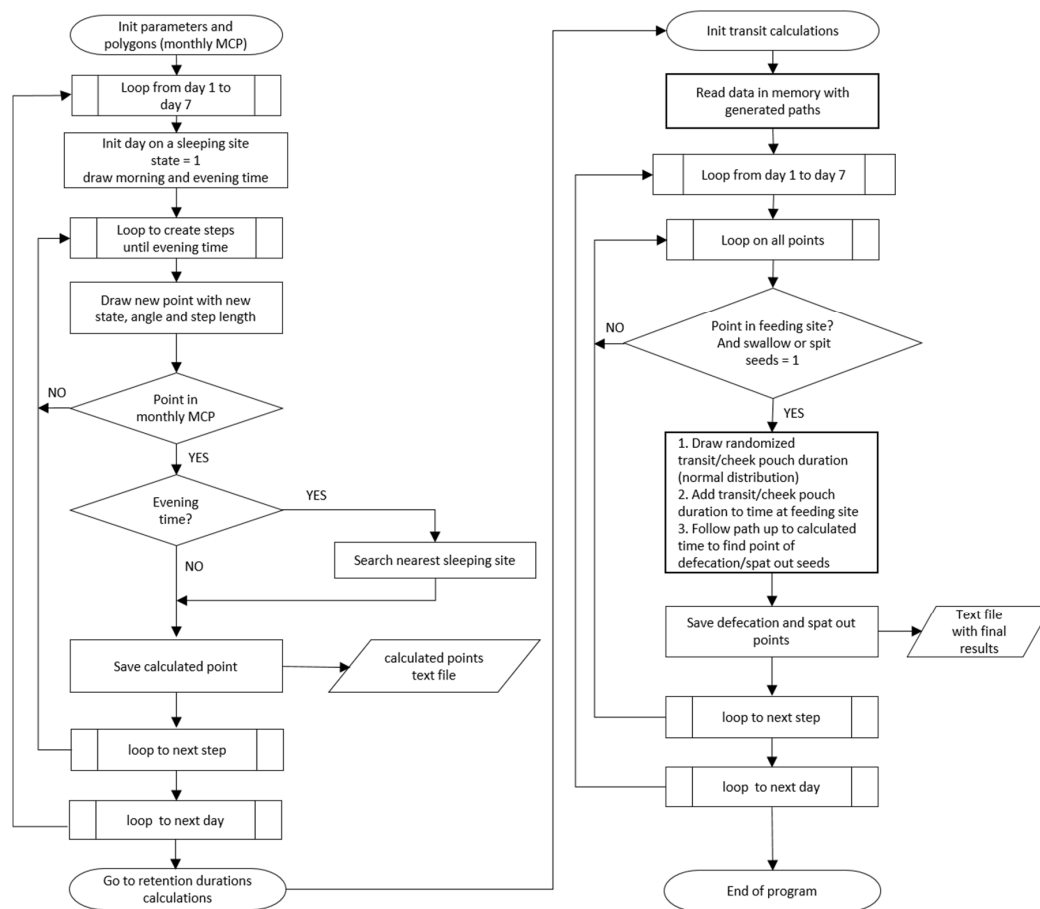


Figure 1. Mechanistic Model of Seed Transfer (MOST) algorithm used in Fortran program for northern pigtailed macaques in Sakaerat.

The model initiated a simulation for retention in relation to seed swallowing or storing into cheek pouches if the generated positions of the troop were within 25 m of an important feeding site coordinates and according to consumed species (i.e., fruit parts eaten and processing methods) and/or season (Table A2). Since macaques did not often reuse their feeding sites during consecutive days (cf. probability of reuse: 0.08), we gave them an equal reuse-frequency. As it was not possible to estimate the quantity of seeds dispersed by macaques in our study, we considered that the simulation retained only one seed in the gut and/or cheek pouch. Any time the simulated path fell within an important feeding site, movement was halted for 10 min to simulate the duration of feeding behavior. We could only collect gut and cheek pouch retention times in situ for a limited number of fruit species with small sample sizes (see results Section 3.3). We then pooled all observed data to simulate gut and cheek pouch retention time for all consumed fruit species. We conducted an a priori examination of

the observed distribution in gut and cheek pouch retention time (Shapiro-Wilk normality test) and concluded a normal distribution. For retention simulations, the procedure drawn random values within the 95% confidence interval of the Gaussian distribution; we recorded positions of the rejected seeds and corresponding parent trees. We recorded the simulated spatial dispersal kernels (i.e., frequency distribution of dispersed seeds relative to distance from parent plants) by calculating the distances between the feeding and the defecation or spitting sites. Thereafter, we estimated the cumulative seed shadow for swallowed and spat out seeds in all species consumed at the important feeding sites to reflect the structural composition and spatial patterns of plant assemblages across macaques' monthly home ranges and seasons. Additionally, we estimated seed shadow of a subset of three trees and one liana species, with medium and large seeds, to illustrate species specific variability (i.e., seasonal distribution and availability, plant traits, seed treatments). We selected these four plant species among the most consumed within macaques' diet or with the highest preference indices (based on the species relative consumption over the species relative availability, following Sengupta et al. [50]) and either abundant or rare across macaques' home range.

To test if the number of simulated seed deposition in DEF and plantations corresponded to the observed macaques' percentage of use of DEF and plantations, we ran chi-squared goodness-of-fit tests with expected ratios set at 85% and 15%, respectively (ratios based on the known occupancy of both forest types by macaques, see results Section 3.1). We used standardized residuals to determine which observed frequencies significantly differed from the expected ones [51].

3. Results

3.1. Ranging, Movement Patterns and Seasonality

Across the 12 study months, observed monthly home range showed wide size variation with a mean of $365.1 \pm \text{SD } 209.3$ ha (range: 139.8–878.8 ha) and covered a mean of $15.4 \pm \text{SD } 10.1\%$ of the plantation forests (range: 5.5%–38.5%) (Table 1). Mean monthly FAI for DEF was $3 \pm \text{SD } 1.4$ (range: 0.80–5.62). Simulated mean daily path length was $2166 \pm \text{SD } 422$ m (range: 560–3667 m, $N = 8005$), similar to the data we collected in the field (i.e., $2151 \pm \text{SD } 497$ m) [32].

3.2. Feeding Sites and Seed Processing

Over the study periods, $N = 407$ feeding sites were identified ($N = 311$ in the DEF and $N = 96$ in the plantation forests) of which 184 were reused (range: 1–4 reuse frequency of feeding site). In total, macaques ate $N = 107$ fruit species, swallowed the seeds of $N = 59$ species, spat out the seeds of $N = 67$ species, dropped the seeds of $N = 36$ species and crunched the seeds of $N = 31$ species. Although macaques in Sakaerat ate a large variety of fruit species, 86.6% of the fruit feeding observations included: *Acacia* species (12.6%), *Azelia xylocarpa* (6.9%), *Aglaia* species (3.5%), *Leucaena leucocephala* (Lam.) de Wit (3.7%), *Willughbeia edulis* Roxb. (3.7%), *Xerospermum noronhianum* Blume (10.8%), species no. 3 (3.1%) and the most eaten species *Dialium conchinchinense* Pierre (42.3%) (Table 2).

In total, we collected 204 fecal samples; 43 with no visible seeds; 98 with crunched seeds mainly corresponding to *Acacia* species (77%) but also to three unripe fruit species (23%); and 63 feces contained intact seeds. Within feces with intact seeds, we found 27 species with a mean number of $12.4 \pm \text{SD } 20$ seeds per feces, a mean number of $1.4 \pm \text{SD } 0.6$ species per feces and a majority of medium and large seeds (Table 3). More than 30% of the feces containing intact seeds were deposited into plantation forests (i.e., 70% into DEF). Among the total number of intact seeds defecated ($N = 1099$), $N = 490$ (from ten native species) were dispersed into plantations and $N = 609$ (from 23 native species) into DEF (Table 3).

3.3. In Situ Retention Times and Dispersal Distances

We estimated a total mean gut retention time of $1980 \pm \text{SD } 900$ min ($N = 8$), that is, $33 \pm \text{SD } 15$ h, for swallowed (i.e., defecated) seed species: crunched *Acacia* species recognizable thanks to their

undigested orange funicle ($2760 \pm \text{SD } 1074$ min) and two intact native species (Table 3). We also estimated a total mean cheek pouch retention time of $21 \pm \text{SD } 10$ min ($N = 9$) for four spat out seed species (Table 4). Based on two swallowed seed species and eight spat out seed species, we obtained average in situ dispersal distances of respectively 1583.2 ± 320.5 m ($N = 5$) and 82.3 ± 54.3 m ($N = 36$) (Tables 3 and 4).

3.4. Simulation of Monthly Seed Shadows

With the simulations, total mean defecated and spat out dispersal distances were $511.4 \pm \text{SE } 3.8$ m (range: 0–2297 m) and $48.6 \pm \text{SE } 0.5$ m (range: 0–869 m), respectively. There was a wide variation of defecated dispersal distances between months, with the larger in August 2018 (mean = $706.7 \pm \text{SE } 54.3$ m, range: 83–2236 m) and no dispersal event in October 2018, corresponding for both, to low fruit availability months (Table 1, Figure 2). Similarly, we found the largest spat out dispersal distances in August 2018 (mean = $74.9 \pm \text{SE } 8.9$ m, range: 0–844 m) and the smallest one in October 2018 (mean = $32.6 \pm \text{SE } 1.8$ m, range: 0–268 m) (Table 1, Figure 3). Among defecated seeds, 11.6% were dispersed between 0–100 m from the theoretical parent tree while 34.7% of the spat out seeds were dispersed between 0–10 m from the parent tree (Figures 2 and 3).

Over the 12 simulated months, only 5.5% ($N = 1199$) of the total seed deposition happened in plantation forests (for 94.5% dispersed in the DEF; $N = 20,428$), which is significantly less than expected, based on macaque's home range plantation coverage of 15.4% (chi-squared test: $\chi^2 = 1516.7$, $P < 0.001$, $N = 21,627$). In plantation forests, there were proportionally more defecated seeds than spat out ones (6.4% and 5%, respectively). Proportion of defecated and spat out seeds dispersed in plantation forests increased during low or medium fruit availability months in DEF (Table 1). Among defecated seeds into plantation forests, 5% were dispersed from DEF ($N = 436$ seeds from 19 species) and 1.4% from plantations. Among spat out seeds into plantation forests, 1% were dispersed from DEF (i.e., $N = 129$ seeds from 12 species) and 4% from plantations. Overall, 24 native species were dispersed from DEF toward plantation forests (Table A2).

3.5. Simulation of a Species Seed Shadow

We selected four plant species in the troop diet to represent specific seed shadows of swallowed and spat out seeds (Tables 2 and A2): (a) *Dialium conchinchinense*, a near-threatened [52] medium-seeded tree species (length size = 8.8 ± 0.7 mm), favorite consumed species, with a high coverage in the troop home range. (b) *Litsea pierrei*, a least concern [53] large-seeded tree species (length size = 20 ± 2.9 mm), with a high preference index but low coverage in the troop home range. (c) *Willughbeia edulis*, (not evaluated) large-seeded liana species (length size = 15 ± 1.6 mm), abundant into macaques' diet. (d) *Afzelia xylocarpa*, an endangered [54] large-seeded tree species (length size = 36 ± 3.2 mm), with a high preference index but a low coverage.

(a) The total mean defecated dispersal distance in *Dialium conchinchinense* was $567.2 \pm \text{SE } 12.3$ m (range: 0–2297 m) and total mean spat out dispersal distance was $50.6 \pm \text{SE } 1.4$ m (range: 0–869 m) (Figure 4). Over nine simulated months (i.e., January to March and July to December), 7.7% of swallowed seeds and 8% of spat out seeds were dispersed in plantation forests (Figure 5). (b) The total mean defecated dispersal distance of *Litsea pierrei* was $476.6 \pm \text{SE } 32.8$ m (range: 16–1570 m) and total mean spat out dispersal distance was $47.7 \pm \text{SE } 3.8$ m (range: 0–246 m) (Figure 4). Over two simulated months (i.e., March, April), 5.7% of swallowed seeds were defecated in plantation forests and none were spat out in plantations (Figure 5). (c) The total mean defecated dispersal distance in *Willughbeia edulis* was $496 \pm \text{SE } 7.2$ m (range: 0–1777 m) and total mean spat out dispersal distance was $47.8 \pm \text{SE } 1.1$ m (range: 0–513 m) (Figure 4). Over three simulated months (i.e., May to July), 6.1% of swallowed seeds were defecated in plantations and 4.4% of spat out seeds were dispersed in plantations (Figure 5). (d) Finally, macaques did not swallow the large seeds of *Afzelia xylocarpa* but the total mean spat out dispersal distance was $53.7 \pm \text{SE } 2.1$ m (range: 0–632 m) (Figure 4). Over 6 simulated months (i.e., January, July and August to December) 17.3% of spat out seeds were dispersed in plantations (Figure 5).

Table 1. Total monthly home range (HR) size with plantations (PF) coverage (cover.) percentage, monthly Food Abundance Index (FAI) calculated for the Dry-evergreen Forest (DEF), monthly macaque frugivory (Frug.), that is, fleshy and dry fruit consumption, simulated monthly daily path length (DPL) with MOST and total monthly dispersal kernel results for swallowed and spat out seeds: frequencies (freq.), mean distances (dist.) and proportions of dispersed (disp.) seeds in plantation forests (PF).

Months	HR Size (ha)	PF Cover. (%)	DPL (m)	FAI DEF	Frug. (%)	Freq.	Swallow Seeds		Spit Seeds		
							Mean dist. (m)	Disp. in PF (%)	Freq.	Mean dist. (m)	Disp. in PF (%)
January 2018	441.6	22.9	2055.8	3.159 **	76.4	100	613.4	7	215	60.4	34.9
February 2018	446.7	13.9	2171.3	1.49 *	74.1	376	601	12	502	46	5.4
March 2018	513.1	38.7	2201.5	0.796 *	84.6	459	474.7	2.6	662	57.7	2.1
April 2017	256.8	13.3	2222.1	5.62 ***	65.8	559	450.2	3.2	716	42.9	0.1
May 2017	140.7	7.4	2240.4	5.293 ***	86.6	1748	440.7	3.6	2258	54	0.3
June 2017	179.0	5.5	2227.2	3.922 ***	73.8	2616	521.1	8.7	3268	47.1	3.6
July 2017	290.6	6.7	2296.1	2.943 **	79.7	1849	547.1	3.2	2713	45.6	1.3
August 2018	878.8	30.5	2269.3	2.066 *	65.8	67	706.7	38.8	164	74.9	47.6
September 2018	145.6	7.9	2089.3	2.098 *	84.2	156	417.2	1.3	213	44.4	0
October 2018	139.8	7.6	2080.5	1.949 *	77.1	0	NA	NA	591	32.6	0
November 2017	507.7	19.1	2056.8	3.215 **	81.2	261	621.2	18	700	45.1	23.6
December 2017	441.2	11.7	21101	3.326 **	68.9	586	532.1	8.7	848	55.4	14.4

Note: * Low fruit availability periods, ** medium fruit availability periods and *** high fruit availability periods calculated in Gazagne et al. [32].

Table 2. Characteristics of the 107 fruit species included in the diet of the *Macaca leonina* Sakaerat troop.

Species	Family	Life Form	Fruit Type	Seed Category	M-/S-Seeded Fruit	Part Consumed	Process	Feeding Obs.
<i>Acacia auricularis</i>	Mimosaceae	MT	D	Small	M	Seed	C	226
<i>Acacia mangium</i>	Mimosaceae	MT	D	Small	M	Seed	C	410
<i>Azelia xylocarpa</i>	Fabaceae	TT	D	Large	M	Mes, Seed	S, C, D	350
<i>Aglaia</i> sp.	Meliaceae	MT	FP	Large	S	FR	W, S	179
<i>Antiaris toxicaria</i>	Moraceae	TT	FP	Small	M	FR	W, C	4
<i>Artocarpus lacucha</i>	Moraceae	MT	FU	Large	M	FR	S, C	16
<i>Artocarpus</i> sp.	Moraceae	MT	FU	Small	M	FR	W, C	1
<i>Baccaurea ramiflora</i>	Euphorbiaceae	ST	FP	Large	M	FR	W, S, D	2
<i>Beilschmiedia</i> sp.	Lauraceae	MT	FU	Large	S	FR	S, D	2
<i>Calamus siamensis</i> becc.	Arecaceae	HE	FP	Medium	S	FR	W, S, C	21
<i>Canarium subulatum</i> guillaumin	Burseraceae	MT	FU	Large	S	FR	S, D	24
<i>Caryota bacsonensis</i> Magalon	Arecaceae	SH	FU	Medium	S	FR	C	5

Table 2. Cont.

Species	Family	Life Form	Fruit Type	Seed Category	M/S-Seeded Fruit	Part Consumed	Process	Feeding Obs.
<i>Cinnamomum porrectum</i>	Lauraceae	MT	FU	Medium	S	FR	-	3
<i>Cissus javana</i>	Vitaceae	SH	FP	Small	S	FR	W	2
<i>Dehaasia cand.</i>	Lauraceae	MT	FU	Large	S	FR	S, D	16
<i>Dialium conchinchinense</i>	Fabaceae	TT	FU	Medium	S	FR	W, S, C	2137
<i>Diospyros castanea</i>	Ebenaceae	MT	FU	Large	M	FR	S, C	-
<i>Diospyros rhodocalyx</i>	Ebenaceae	MT	FU	Large	M	FR	W, S, C	2
<i>Diospyros</i> sp. 1	Ebenaceae	MT	FU	Large	M	FR	W, S, C	6
<i>Diospyros</i> sp. 2	Ebenaceae	MT	FU	Large	M	FR	W, S, C	4
<i>Dysoxylum cyrtobotryum</i>	Meliaceae	ST	FP	Large	M	FR	-	-
<i>Ficus altissima</i>	Moraceae	TT	FU	Small	M	FR	W	2
<i>Ficus macrophylla</i>	Moraceae	TT	FU	Small	M	FR	W	-
<i>Ficus</i> spp.	Moraceae	TT	FU	Small	M	FR	W	-
<i>Garaga pinnata</i>	Meliaceae	MT	FP	Medium	S	FR	W, S	3
<i>Garcinia cowa</i>	Clusiaceae	MT	FU	Large	M	FR	W, S	-
<i>Garcinia speciose</i>	Clusiaceae	MT	FU	Large	M	FR	W, S, C	1
<i>Glycosmis pentaphylla</i>	Rutaceae	ST	FU	Small	S	FR	W, S, C	4
<i>Gonocaryium lobbianum</i>	Cardiopteridaceae	ST	FU	Large	S	FR	D	-
<i>Hydnocarpus ilicifolia</i>	Achariaceae	ST	FP	Medium	M	Mes, Seed	C, D	5
<i>Hypobathrum racemosum</i>	Rubiaceae	ST	FU	Medium	S	FR	W, S	10
<i>Irvingia malayana</i>	Irvingiaceae	TT	FU	Large	S	FR	D	-
<i>Knema globularia</i>	Myristicaceae	ST	FP	Large	S	FR	W, S, D	15
<i>Knema linifolia</i>	Myristicaceae	MT	FP	Medium	S	FR	W, S, D	20
<i>Leucaena leucocephala</i>	Fabaceae	MT	D	Small	M	Mes, Seed	C	145
<i>Litsea pierrei</i>	Lauraceae	MT	FU	Large	S	FR	W, S, D	37
<i>Mangifera</i> sp.	Anacardiaceae	MT	FU	Large	S	FR	D	13
<i>Melia azedarach</i>	Meliaceae	MT	FU	Large	S	FR	S, D	-
<i>Melodorum fruticosum</i>	Annonaceae	ST	FU	Medium	S	FR	W, S	7
<i>Memecylon ovatum</i>	Melastomataceae	ST	FU	Medium	S	FR	W, S	38
<i>Memecylon scutellatum</i>	Melastomataceae	ST	FU	Medium	S	FR	W, S	29
<i>Memecylon</i> sp.	Melastomataceae	ST	FU	Medium	S	FR	W, S	3
<i>Microcos tomentosa</i>	Malvaceae	MT	FU	Medium	S	FR	W, S	17
<i>Micromelum minutum</i>	Rutaceae	ST	FU	Small	S	FR	W, S	12
<i>Miliusa lineata</i>	Annonaceae	MT	FP	Medium	M	FR	S	-
<i>Nephelium hypoleucum</i>	Sapindaceae	MT	FP	Large	S	FR	W, S, D	9
<i>Parkia sumatrana</i>	Fabaceae	TT	D	Large	M	Mes	S, D	27
<i>Peltophorum pterocarpum</i>	Fabaceae	MT	D	Medium	M	Mes, Seed	C	11
<i>Polyathia cerasoides</i>	Annonaceae	ST	FU	Small	S	FR	W, S	3

Table 2. Cont.

Species	Family	Life Form	Fruit Type	Seed Category	M/S-Seeded Fruit	Part Consumed	Process	Feeding Obs.
<i>Prunus javanica</i>	Rosaceae	TT	FU	Medium	S	FR	W, S	4
<i>Rourea minor</i> Leenh	Connaraceae	SH	FP	Large	S	FR	W, S, D	8
<i>Rutaceae</i> sp.	Rutaceae	ST	FP	Small	S	FR	W, S	25
<i>Salacia chinensis</i>	Celastraceae	LI	FP	Large	M	FR	W, S, D	10
<i>Salacia verrucosa</i>	Celastraceae	LI	FP	Large	M	FR	W, S, D	10
<i>Sapotaceae</i> sp.	Sapotaceae	TT	FU	Large	M	FR	W, S, D	63
<i>Schleichera oleosa</i>	Sapindaceae	MT	FU	Large	S	FR	S	9
<i>Spondias pinnata</i>	Anacardiaceae	MT	FU	Large	S	FR	S, C, D	2
<i>Streptocaulon juvenas</i>	Apocynaceae	LI	D	Medium	S	Seed	C	28
<i>Syzygium cumini</i>	Myrtaceae	MT	FU	Small	S	FR	W, S	1
<i>Syzygium siamense</i>	Myrtaceae	ST	FU	Large	M	FR	C, D	-
<i>Syzygium</i> sp. 1	Myrtaceae	MT	FU	Small	S	FR	W	19
<i>Syzygium</i> sp. 2	Myrtaceae	MT	FU	Large	S	FR	S, D	18
<i>Syzygium</i> sp. 3	Myrtaceae	LT	FU	Large	S	FR	S, D	7
<i>Suregada multiflora</i>	Euphorbiaceae	MT	FU	Large	M	FR	S, D	3
<i>Toddalia asiatica</i>	Rutaceae	LI	FP	Small	M	FR	W	7
<i>Uvaria cordata</i>	Annonaceae	SH	FP	Large	M	FR	W, S	-
<i>Vitex quinata</i>	Lamiaceae	ST	FU	Medium	S	FR	W, S, D	32
<i>Walsura trichostemon</i>	Meliaceae	ST	FP	Medium	S	FR	W, S	2
<i>Willughbeia edulis</i>	Apocynaceae	SH	FP	Large	M	FR	W, S, D	188
<i>Xerospermum noronhianum</i>	Sapindaceae	MT	FP	Large	S	FR	W, S, D	546
Species no. 1	Herbaceae	HE	FU	Small	S	FR	W	5
Species no. 2	Apocynaceae	LI	D	Large	M	Seed	C	2
Species no. 3	-	LI	FP	Large	M	FR	W, S, C, D	159
Species no. 4	-	LI	FU	Medium	S	FR	S	2
Species no. 5	-	SH	FU	Medium	S	FR	W	1
Species no. 6	-	-	FU	Large	S	FR	S, D	1
Species no. 7	-	T	FU	Medium	S	FR	W	3
Species no. 8	-	T	FP	Medium	S	FR	S	1
Species no. 9	Dipterocarpaceae	T	D	Medium	S	Seed	C	1
Species no. 10	-	-	D	Medium	S	Seed	C	2
Species no. 11	-	T	FP	Medium	M	FR	W, C	9
Species no. 12	Sapindaceae	T	FP	Large	S	FR	W, S, D	12
Species no. 13	Fabaceae	-	D	Large	M	Mes, Seed	C	1
Species no. 14	Apocynaceae	LI	FP	Large	M	FR	W, S, C, D	17
Species no. 15	-	TT	FU	Large	S	FR	W, S	4
Species no. 16	-	LI	FP	Large	M	FR	W, S	1

Table 2. Cont.

Species	Family	Life Form	Fruit Type	Seed Category	M-/S-Seeded Fruit	Part Consumed	Process	Feeding Obs.
Species no. 17	-	ST	FU	Small	S	FR	W	9
Species no. 18	-	-	FU	Large	S	FR	W, S	5
Species no. 19	-	LI	FP	-	-	-	-	4
Species no. 20	-	LI	FP	Medium	M	FR	W, S, C, D	2
Species no. 21	-	LI	FU	Medium	M	FR	W, S	-
Species no. 22	Annonaceae	MT	FP	Large	M	FR	W, S	5
Species no. 23	-	LI	FU	Large	S	FR	W	-
Species no. 24	-	-	FU	Medium	S	FR	S, D	10
13 unknown species	-	-	-	-	-	FR	W, S, C, D	42

Note: Species no. 1–24 are unidentified. Life forms: HE = herb, LI = liana, SH = shrub, T = tree, ST = small tree (5–15 m), MT = middle-sized tree (15–30 m), TT = tall tree (>30 m). Fruit types: D = dry, FU = fleshy unprotected, FP = fleshy protected. Seed category: seed size with Small < 5 mm, 5 mm < Medium < 10 mm, Large > 10 mm, based on Albert et al. [28]. M-/S- seeded fruit: M = Multi-, S = Single-. Part consumed: FR = fruit, Mes = mesoderm and seed. Processing methods: W = swallow, S = spit out, C = crunch, D = drop. Number of feeding observations via scan sampling, N_{total} fruit feeding observations = 5553. - = no data. Grey shaded rows present the most consumed species.

Table 3. Intact seed species within macaques' feces in Sakaerat: mean size \pm SD, mean number \pm SD, observed mean dispersal distance \pm SD, mean gut retention time \pm SD and forest types in which they were dispersed.

Species	Seed Length (mm)	Seed Width (mm)	Seed Size Category	Number of Seeds	Dispersal Distance (m)	Gut Retention Time (min)	Forest Types
<i>Aglaia</i> sp.	14 \pm 4	10 \pm 2	Large	8.9 \pm 8.7	-	-	DEF
<i>Dialium conchinchinense</i>	8.8 \pm 0.7	6.7 \pm 0.7	Medium	10.7 \pm 7.1	1584 \pm 394	1542 \pm 234	DEF; PF
<i>Garaga pinnata</i>	8.5 \pm 0.5	7 \pm 0	Medium	1 \pm 0	-	-	DEF; PF
<i>Knema globularia</i>	10.6	10.1	Large	2.3 \pm 1.9	-	-	DEF
<i>Listea pierrei</i>	16 \pm 0	8.7 \pm 0.5	Large	3	-	-	DEF
<i>Melodorum siamensis</i>	7.8 \pm 0.9	4.2 \pm 0.4	Medium	3.3 \pm 2.1	-	-	PF
<i>Microcos tomentosa</i>	6 \pm 3	6 \pm 2	Medium	24 \pm 20.4	-	-	DEF; PF
<i>Nephelium hypoleucum</i>	17.5 \pm 0.5	9.5 \pm 0.5	Large	2	-	-	DEF
<i>Toddalia asiatica</i>	4.3 \pm 0.5	2.9 \pm 0.4	Small	55 \pm 37	1582 \pm 319	1518 \pm 171.7	DEF; PF
<i>Uvaria cordata</i>	18	11	Large	1	-	-	PF
<i>Salacia</i> sp.	15 \pm 0	10 \pm 0	Large	2	-	-	DEF
Sapotaceae sp.	14.4 \pm 0.6	8.6 \pm 1	Large	2	-	-	DEF
<i>Vitex quinata</i>	10	6	Large	1	-	-	DEF
<i>Willughbeia edulis</i>	15 \pm 1.6	11 \pm 2	Large	6.1 \pm 4.4	-	-	DEF; PF
<i>Xerospermum noronhianum</i>	21 \pm 1	14 \pm 0.8	Large	2.5 \pm 0.5	-	-	DEF
Species no. 3	13 \pm 1.1	11 \pm 1.3	Large	13 \pm 10	-	-	DEF; PF
Species no. 12	15	10	Large	3	-	-	DEF
Species no. 14	12 \pm 3	7 \pm 2	Large	4 \pm 1	-	-	DEF
Species no. 15	27	19	Large	1	-	-	DEF
Species no. 16	11 \pm 0	6.7 \pm 0.5	Large	3	-	-	DEF

Table 3. Cont.

Species	Seed Length (mm)	Seed Width (mm)	Seed Size Category	Number of Seeds	Dispersal Distance (m)	Gut Retention Time (min)	Forest Types
Species no. 18	16 ± 0.8	13 ± 4.5	Large	3	-	-	PF
Species no. 22	10 ± 1	6.5 ± 0.5	Large	2	-	-	DEF
Species no. 23	16 ± 0	8 ± 0	Large	2	-	-	DEF
Species no. 25	13 ± 1.6	9.3 ± 0.6	Large	5	-	-	DEF
Species no. 26	0.8	0.5	Medium	1	-	-	DEF
Species no. 29	7	7	Medium	1	-	-	PF
Species no. 30	9.3 ± 1.1	5.4 ± 0.8	Medium	3.7 ± 1.2	-	-	DEF

Note: Species no. 3-30 are unidentified. Seed size category (small, medium or large) is based on Albert et al. [28]. - = no data. Abbreviation: DEF, dry-evergreen forest; PF, plantation forests.

Table 4. Intact seed species spat out by macaques in Sakaerat: mean size ± SD, mean number ± SD, observed mean dispersal distance ± SD, mean cheek pouch retention time ± SD.

Species	Seed Length (mm)	Seed Width (mm)	Seed Size Category	Number of Seeds	Dispersal Distance (m)	Cheek Pouch Retention Time (min)
<i>Azelia xylocarpa</i>	37 ± 3.2	18 ± 1.6	Large	3	87.3 ± 31.6	20.5 ± 12.5
<i>Aglaia</i> sp.	14 ± 4	10 ± 2	Large	8.9 ± 8.7	38 ± 5.9	12.3 ± 2.9
<i>Beilschmiedia</i> sp.	16	8	Large	1	-	-
<i>Artocarpus lacucha</i>	13 ± 1	10 ± 1	Large	-	-	-
<i>Beilschmiedia</i> sp.	14 ± 2	9 ± 1	Large	-	-	-
<i>Dehaasia candolleana</i>	21 ± 4	10 ± 1	Large	-	-	-
<i>Dialium conchinchinense</i>	8.3 ± 0.7	6.7 ± 0.5	Medium	11	81.1 ± 53	25 ± 7
<i>Listea pierrei</i>	20.3 ± 0.9	10.3 ± 0.9	Large	1.5 ± 0.5	-	-
<i>Memecylon ovaton</i>	6 ± 0	6 ± 0	Medium	19	132 ± 11.5	30.5 ± 3.5
<i>Uvaria cordata</i>	17 ± 3	12 ± 4	Large	5 ± 0	-	-
<i>Spondias pinnata</i>	34 ± 3	26 ± 1	Large	-	-	-
<i>Syzygium</i> sp. 3	19 ± 1.5	16 ± 1.9	Large	-	10	-
<i>Vitex quinata</i>	8.5 ± 0.5	6.2 ± 0.7	Medium	6	16 ± 5	-
<i>Willughbeia edulis</i>	15 ± 1.6	13 ± 2	Large	6.5 ± 0.5	-	-
<i>Xerospermum noronhianum</i>	21 ± 1	14 ± 0.8	Large	26.2 ± 46.5	-	-
Species no. 3	13 ± 1.1	11 ± 1.3	Large	13 ± 10	-	-
Species no. 12	15	10	Large	3	159.7 ± 11.8	-
Species no. 14	12 ± 3	7 ± 2	Large	4 ± 1	-	-
Species no. 15	27	19	Large	-	-	-
Species no. 16	11 ± 0	6.7 ± 0.5	Large	3	-	-
Species no. 18	16 ± 0.8	13 ± 4.5	Large	3	-	-
Species no. 22	10 ± 1	6.5 ± 0.5	Medium	2	28.5 ± 3.5	-
Species no. 24	6.9 ± 0.7	5.4 ± 0.4	Medium	-	-	-
Species no. 28	24	18	Large	-	-	-

Note: Species no. 3–28 are unidentified. Seed size category (small, medium or large) is based on Albert et al. [28]. - =no data.

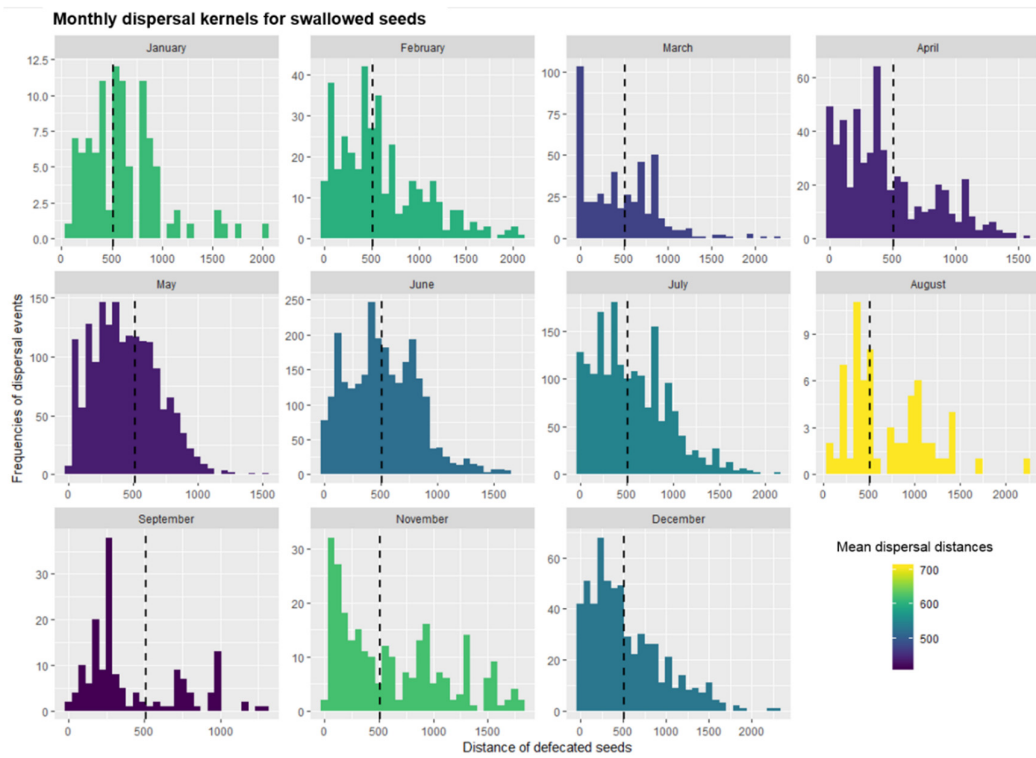


Figure 2. Simulated monthly total dispersal kernels for swallowed seeds by the northern pigtailed macaques inhabiting the degraded forest fragment of Sakaerat. The dash line represents the total mean dispersal distance = 511 m.

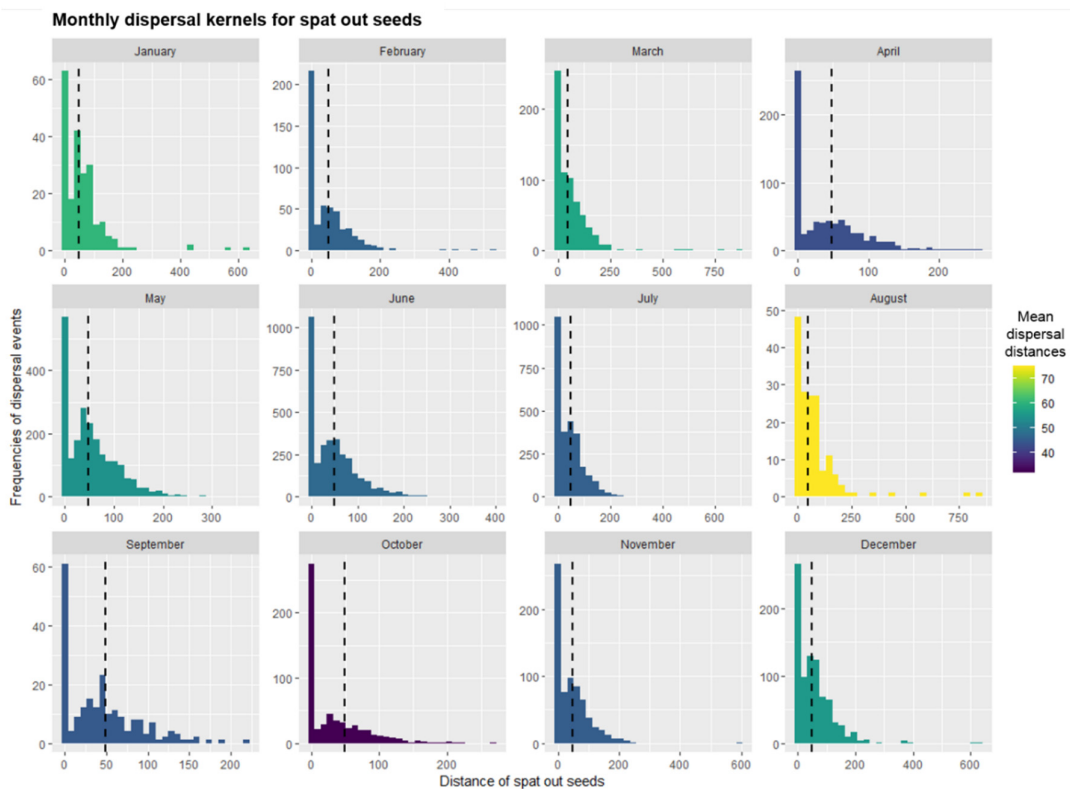


Figure 3. Simulated monthly total dispersal kernels for spat out seeds by the northern pigtailed macaques inhabiting the degraded forest fragment of Sakaerat. The dash line represents the total mean dispersal distance = 49 m.

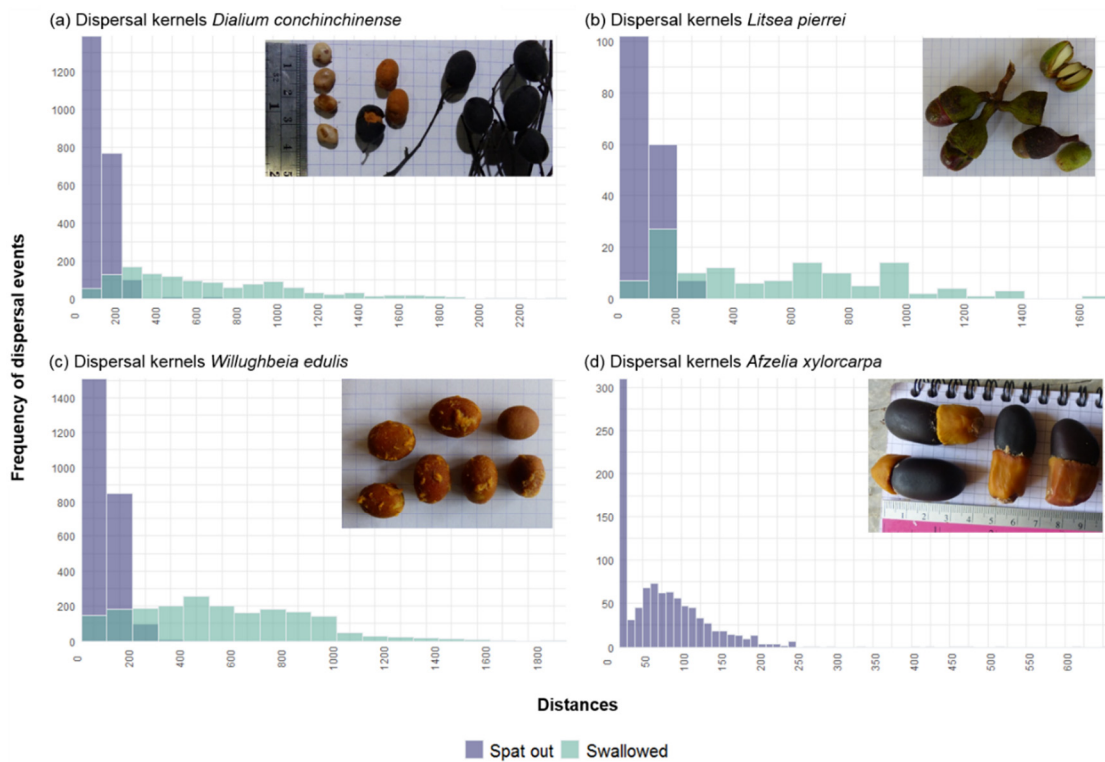


Figure 4. Simulated dispersal kernels for swallowed and spat out seeds in four plant species consumed by the northern pigtailed macaques in Sakaerat: (a) *Dialium conchinchinense*, (b) *Listea pierrei*, (c) *Willughbeia edulis* and (d) *Afzelia xylocarpa*. Note: The dark green color is the result of the juxtaposition of the spat out and swallowed dispersal kernels.

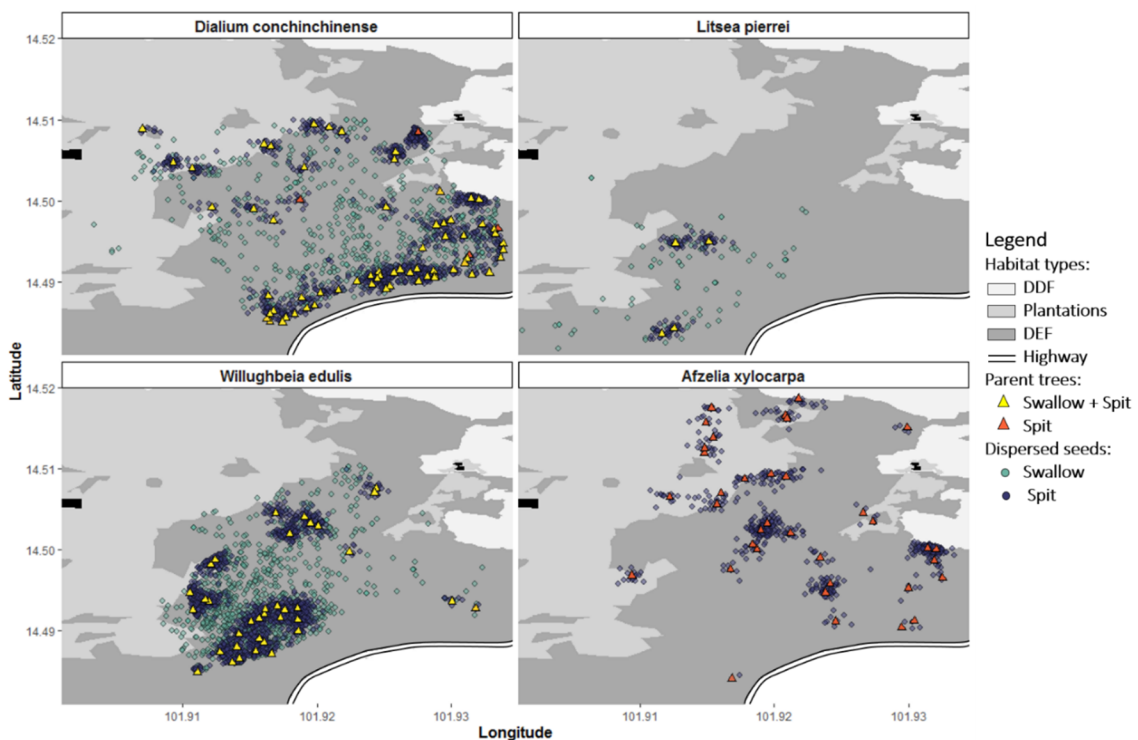


Figure 5. Spatial distribution of the simulated dispersed seeds of the selected species via swallowing (defecated) or cheek pouch (spat out) by the northern pigtailed macaques within the degraded forest fragment of Sakaerat.

4. Discussion

Our study aimed to investigate the seed shadows of northern pigtailed macaques by combining field-collected data and seed deposition modeling techniques. We found seed shadows characteristic of effective seed dispersers in a degraded habitat: macaques dispersed a high number of medium- and large-seeded species both within the native forest (DEF) and toward the plantations and produced highly leptokurtic dispersal kernels (i.e., with a peak at or close to the parent plant, followed by a rapid decline and a long and relative fat tail) indicating relatively high levels of long-distance dispersal [55,56].

4.1. Seed Dispersal Effectiveness in Degraded Habitats

4.1.1. Seed Category and Treatment

Ideally, for the regeneration of degraded habitats, seeds dispersed should include early-, mid- and late-successional species [57]. Unfortunately, few large-seeded and shade-tolerant species, critical to drive late-successional stages, are generally brought into degraded areas [11,58]. In our study, we found that northern pigtailed macaques were likely to disperse (via swallowing or spitting) at least 76 seed species, undamaged by retention in mouth and gut, with ~80% of medium- and large-sized seeds (Table 2). We found a lot of destroyed seeds in macaques' feces (48%), mostly coming from exotic trees such as *Acacia* seeds, that macaques used as fallback foods during low native fruit availability [32,59]. Similar to rhesus macaques (*Macaca mulatta*) inhabiting a moderately disturbed forest in Northern India [27], northern pigtailed macaques predate on *Acacia* species, therefore preventing the likelihood of dispersing exotic species toward native forests, while dispersing native species into old growth plantation forests. However, the noteworthy proportion of predation on unripe native seed species was likely due to low fruit availability in the degraded forest fragment and to related intra-group feeding competition leading to unripe fruit consumption by lower-ranking individuals, who could not access the ripe fruits [60].

4.1.2. Seed Shadow Simulations

Cercopithecine species are known to spit out seeds on the feeding site, often under the parent plant [24,61]. However, dispersal distances larger than 10 m from the parent plant are supposed to allow escaping density-dependent mortality under parent crowns [62,63]. Our simulations showed that 65% of the seeds stored in cheek pouches were spat beyond 10 m of the parent tree, with a mean of 49 m. The larger mean dispersal distances for spat out seeds we collected in the field (i.e., 82.3 m) in comparison to the simulated mean dispersal distances probably came from an overestimated mean dispersal distances due to our field methodology. When compared to rhesus macaques in India, the dispersal distances collected for spat out seeds (mean: 19 m) [27] were shorter than in northern pigtailed macaques of Sakaerat.

Long-distance dispersal of plants poses challenges to research because it involves rare events and site- and species-specific components [64]. Dispersal distance larger than 100 m from the parent tree is generally defined as long-distance dispersal [9,65,66]. However, species such as pigeons and hornbills can disperse at several kilometers between adjacent patches [19]. Our simulations with MOST showed that 88% of the swallowed seeds (defecated) were deposited beyond 100 m, with a mean dispersal distance of 511 m. The in situ dispersal distance validated this large simulated dispersal distance with a mean of 1583 m. This is a considerable long-distance compared to what has been previously reported for macaques. In comparison, the dispersal distances collected for defecated seeds in *Macaca mulatta* inhabiting a moderately degraded habitat was shorter with a mean of 117 m [27]; and the median distances collected for *Macaca fuscata* in Northern Japan was 478 m [67]. Although the simulation for swallowed seeds presented the widest spatial distribution within macaques' home range (Figure 5), we also obtained many seeds defecated under the parent crown, which explained the shorter mean dispersal distances compared to data collected in the field. One reason could be that the model can

reuse the same sleeping and feeding sites, which is not often the case in reality. The reuse of the same resources by our simulations could also explain why we obtained significantly fewer dispersed seeds in plantation forests in comparison to macaques' occupancy percentage to the latter and to the percentage of defecated seeds we observed in plantations (i.e., 44.6% of observed seeds for 6.4% of seeds dispersed in plantations with MOST). The simulated defecation dispersal distances may therefore be underestimated as well as the percentage of seeds dispersed into plantation forests. To evaluate the model success, further studies should also simulate the seed shadows based on animal's movement (collected every minute) and feeding behavior (see algorithm proposed in Figure A1) and compare them with the simulated seed shadows obtained with MOST.

Ideally, seed shadows for each fruit species should be estimated based on their specific retention times. However, the reality of the field conditions makes it extremely difficult. Although we used random values corresponding to a Gaussian distribution, we found fruit species-specific seed shadows, based on monthly consumption probability, feeding site distribution and seed treatments (i.e., swallowed, spat out, crunched). Overall, for all fruit species studied, we observed complementary seed depositions (thanks to different macaques' handling methods) and wide seasonal seed shadow variations for defecated and spat seeds. These findings present quite realistic seed shadows for plant communities dispersed by a frugivorous primate species. Our study highlights the importance of accounting for seasonal variation in (a) movement (i.e., with the use of the Hidden Markov Model including monthly variation of FAI), (b) resource availability and distribution (e.g., sleeping and feeding sites) [67], (c) photoperiod, as well as (d) macaque feeding behavior with seasonal seed treatments according to fruit maturity (e.g., destroying seeds when fruits were immature or old), in order to produce seasonal seed shadows. Finally, MOST can be improved by including monthly frequency and duration of feeding site use, to account for seasonal variation in foraging behavior.

4.1.3. Macaques as Effective Seed Dispersers in Degraded Habitats?

We estimated that macaques generated extensive seed shadows of various plant species with high levels of long-distance dispersal. They are medium-bodied frugivores but several studies showed that body size does not affect dispersal distances [22,26,29]. The relative long dispersal distances we found were probably related to macaques' long retention times, combined with their spread out movement patterns affected by low native fruit availability in the degraded forest fragment [32]. In contrast, macaques inhabiting primary forests with high and clumped fruit availability or food provisioning, can potentially present reduced seed shadows [68]. Overall, our results suggest that the role of macaques as reliable seed dispersers over long distances has been underestimated, in comparison to other medium and large Asian primates such as gibbons and orangutans [23].

In accordance with our hypotheses, macaques dispersed a large majority of medium- and large-seeded native fruits, at substantial distances from their parent plants in native forests and plantations, increasing the likelihood to deposit large seeds in suitable patterns and places for their survival and germination in degraded areas. Additionally, they dispersed seeds from at least 24 native species from native forests to plantations, with 5.5% of the seeds deposited in plantation forests. Although our simulations present a low percentage of seeds dispersed into plantations, it has been shown that even a few large tree seeds meaningfully contribute to seedling recruitment [69], which could significantly impact future changes into stand composition and structure into plantations. Therefore, we conclude that northern pigtailed macaques are effective seed dispersers in degraded habitats and likely play a crucial role in native forest maintenance and plantation forest regeneration. However, an in-depth investigation of the composition and distribution of seedling recruitment in both forest types would help to empirically confirm the macaque seed dispersal effectiveness. Further studies should use MOST combined with dynamic vegetation models in order to generate 'true-life' defecation and spitting patterns [33]. It could be useful to test tree species survival by simulating tree regeneration and growth at local scale through macaques' seed dispersal services.

Finally, given the macaques' flexible behavior and sometimes fission-fusion dynamics [70,71], dispersing groups are more likely to range far away in their habitat, over deforested and open areas and to cross roads [24]. Under these circumstances, they could introduce new and/or large-seeded species not only within degraded forest fragments but also between adjacent forest patches, allowing connectivity between fragmented populations and colonization of new degraded habitats [9].

4.2. Conservation Implications

Diversity and availability of large-seeded species, often late-successional plant families, are the most affected by habitat degradation [16,57]. We found that northern pigtailed macaques could effectively disperse and contribute to the persistence of one of their preferred species, *Afzelia xylocarpa*, an endangered large-seeded tree species of socio-economic benefits to local communities for its high timber value and use in traditional medicine [72]. Additionally, northern pigtailed macaques are classified as vulnerable by the IUCN Red List, due to habitat degradation, trade and hunting [73]. Their extinction in small forest fragments could result in significant changes in vegetation diversity and spatial community structure and reduce forest maintenance capacity and regeneration [21]. Our findings highlight the importance of protecting these animals as local umbrella species and raising awareness of local human communities about macaques' facilitating ecosystem services in management plans for forest restoration and regeneration.

5. Conclusions

Addressing seed shadows under field condition is extremely challenging. We present here a relatively effective method with the dispersal module MOST, to simulate realistic seed shadows of a frugivore based on its feeding behavior, movement patterns and monthly resource availability. We estimated the longest dispersal distance events ever reported for macaques, with complementary seed shadows for medium to large seeds, contributing to forest regeneration and maintenance in a degraded forest fragment. However, to fully understand the relative role that macaques play in plant species seed rain and seed shadows, as well as plant community assembly in degraded habitats, further research should study the plant species dispersed by macaques in a community-level approach and integrate the post-dispersal fate of spat and defecated seeds into models [10,74].

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Appendix A

Table A1. Observed monthly entry and exit times to and from sleeping sites for the northern pigtailed macaques inhabiting the degraded forest of Sakaerat.

Months	Entry Time	Exit Time
January 2018	18 h 09 min ± SD 8	06 h 44 min ± SD 8
February 2018	18 h 22 min ± SD 5	06 h 39 min ± SD 3
March 2018	18 h 25 min ± SD 7	06 h 36 min ± SD 9
April 2017	18 h 17 min ± SD 9	06 h 14 min ± SD 9
May 2017	18 h 36 min ± SD 5	06 h 20 min ± SD 16
June 2017	18 h 28 min ± SD 11	05 h 58 min ± SD 10
July 2017	18 h 47 min ± SD 10	06 h 02 min ± SD 7
August 2018	18 h 23 min ± SD 10	06 h 17 min ± SD 10
September 2018	18 h 08 min ± SD 9	06 h 09 min ± SD 11
October 2018	17 h 55 min ± SD 7	06 h 09 min ± SD 03
November 2017	17 h 39 min ± SD 7	06 h 25 min ± SD 12
December 2017	17 h 52 min ± SD 2	06 h 17 min ± SD 3

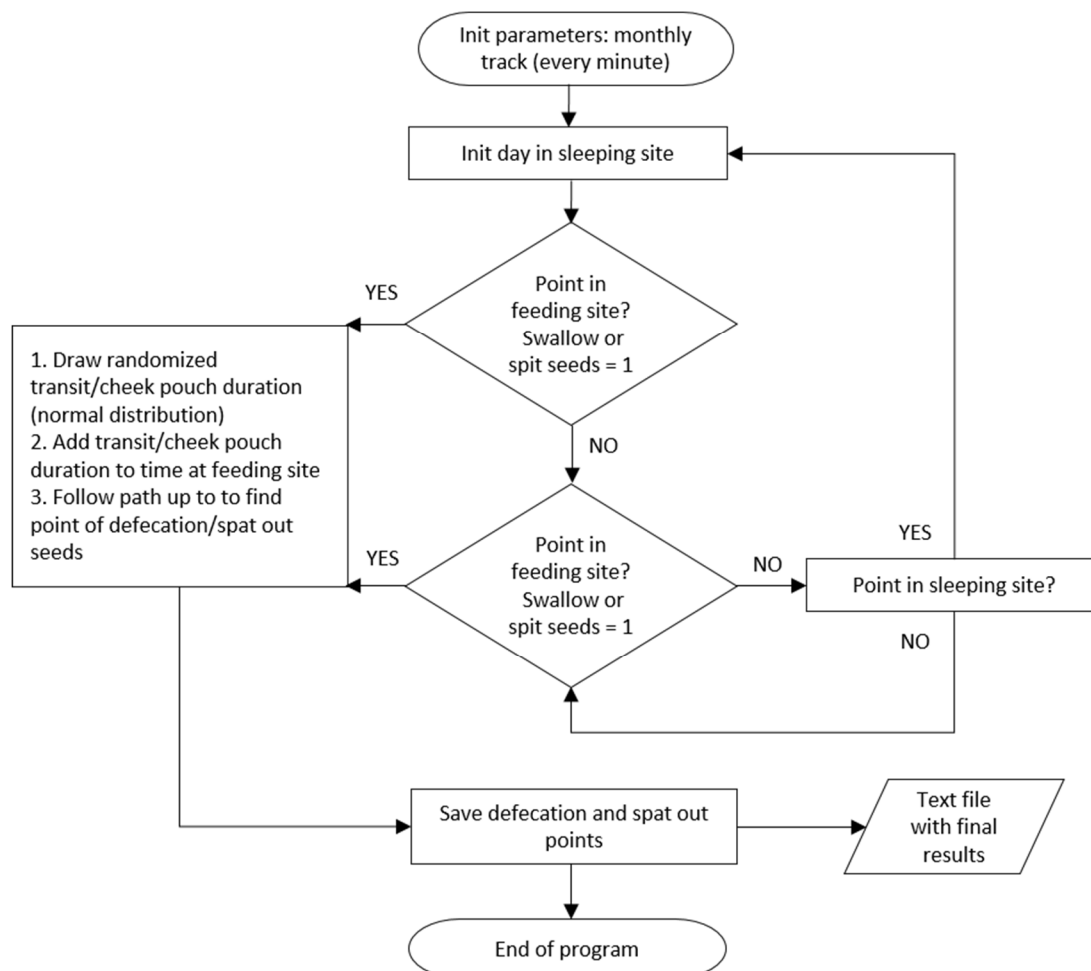


Figure A1. Model of seed transfer to estimate seed shadows based on northern pigtailed macaques' movement pattern and resource use in Sakaerat.

Table A2. Main plant species in northern pigtailed macaques' important feeding sites in Sakaerat used by MOST over the 12 simulated months, with frequencies of dispersed seeds in Dry-Evergreen Forest (DEF) or Plantation Forests (PF) and their processing methods (swallowed or spat out) according months.

Species	Stat	Cov.	Pref.	Forest Types	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sept.	Oct.	Nov.	Dec.
<i>Azalia xylocarpa</i>	EN	0.25	4.47	DEF (622) PF (105)	S (37)	-	-	-	-	-	S (462)	S (42)	S (81)	-	S (51)	S (54)
<i>Aglaia</i> sp.	-	0.7	4.07	DEF (2099) PF (59)	-	-	-	-	W (76) S (102)	W (478) S (660)	W (352) S (490)	-	-	-	-	-
<i>Artocarpus lacucha</i>	NE	0.2	0.36	DEF (0) PF (1)	-	-	S (1)	-	-	-	-	-	-	-	-	-
<i>Baccaurea ramiflora</i>	LC	-	-	DEF (20) PF (1)	-	-	W (10) S (11)	-	-	-	-	-	-	-	-	-
<i>Canarium subulatum guillaumin</i>	NE	0.05	7.64	DEF (7) PF (1)	-	-	-	W (2) S (6)	-	-	-	-	-	-	-	-
<i>Dehaasia candolleana</i>	NE	0.1	0.85	DEF (117) PF (12)	-	-	S (129)	-	-	-	-	-	-	-	-	-
<i>Dialium conchinchinense</i>	NT	0.65	22.92	DEF (2040) PF (244)	W (100) S (102)	W (35) S (44)	W (23) S (32)	-	-	-	W (114) S (149)	W (21) S (23)	W (54) S (54)	S (591)	W (217) S (309)	W (542) S (728)
<i>Diospyros</i> sp.	-	0.6	0.17	DEF (148) PF (26)	-	-	-	-	-	-	W (62) S (87)	W (10) S (15)	-	-	-	-
<i>Garaga pinnata</i>	NE	-	-	DEF (30) PF (4)	-	-	-	-	-	-	-	W (11) S (23)	-	-	-	-
<i>Knema globularia</i>	LC	0.25	0.14	DEF (92) PF (2)	-	-	-	W (11) S (13)	-	W (34) S (36)	-	-	-	-	-	-
<i>Litsea pierrei</i>	LC	0.1	2.95	DEF (199) PF (5)	-	-	W (40) S (47)	W (44) S (73)	-	-	-	-	-	-	-	-
<i>Memecylon ovatum</i>	LC	0.55	0.22	DEF (440) PF (6)	-	-	-	-	-	W (5) S (7)	W (183) S (241)	W (5) S (5)	-	-	-	-
<i>Memecylon scutellatum</i>	NE	0.25	0.66	DEF (86) PF(2)	-	-	-	W (39) S (49)	-	-	-	-	-	-	-	-
<i>Microcos tomentosa</i>	LC	0.65	0.07	DEF (11) PF (39)	-	-	-	-	-	-	-	-	-	-	W (22) S (28)	-
<i>Salacia</i> sp.	-	-	-	DEF (171) PF (2)	-	-	-	-	-	W (22) S (34)	W (53) S (64)	-	-	-	-	-
<i>Sapotaceae</i> sp.	-	0.55	0.95	DEF (150) PF (12)	-	-	-	-	-	-	-	-	-	-	W (22) S (51)	W (35) S (54)
Species no. 3	-	-	-	DEF (1568) PF (80)	-	W (341) S (458)	W (386) S (442)	-	-	-	-	-	-	-	-	W (9) S (12)
Species no. 11	-	-	-	DEF (11) PF(0)	-	-	-	-	-	-	W (11) S (304)	-	-	-	-	-
Species no. 12	-	-	-	DEF (507) PF (24)	-	-	-	-	-	-	W (227) S (304)	-	-	-	-	-
<i>Spondias pinnata</i>	NE	0.15	0.21	DEF (15) PF (104)	S (76)	-	-	-	-	-	-	S (7)	-	-	S (36)	-
<i>Syzygium</i> sp.	-	0.4	0.4	DEF (664) PF (17)	-	-	-	W (35) S (41)	W (58) S (73)	W (198) S (276)	-	-	-	-	-	-
<i>Vitex quinata</i>	LC	0.15	2.55	DEF (250) PF (52)	-	-	-	-	-	-	-	W (20) S (49)	W (102) S (131)	-	-	-
<i>Willughbeia edulis</i>	NE	-	-	DEF (2919) PF (182)	-	-	-	-	W (394) S (508)	W (719) S (895)	W (280) S (305)	-	-	-	-	-
<i>Xerospermum noronhianum</i>	NE	0.15	4.79	DEF (6092) PF (185)	-	-	-	W (428) S (534)	W (1220) S (1575)	W (1160) S (1360)	-	-	-	-	-	-

Note: Species no. 3, 11 and 12 are unidentified. Stat = IUCN status (LC: Least Concern, NT: Near Threatened, EN: Endangered; NE: Not Evaluated); Cov. (Coverage) = number of botanical plots with the tree species/total number of botanical plots; Pref. (Preference indices) = ratio of number of feeding scans for the consumed species to the total number of feeding scans/ratio of number of stems for the consumed species of the total number of stems into the botanical plots. Preference indices >1 indicate a preference for a fruit family [50]; - = no data; Processing methods: W = swallow, S = spit out. Grey shaded rows present the species used for the simulations of a species seed shadow using the mechanistic Model of Seed Transfer (MOST).

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