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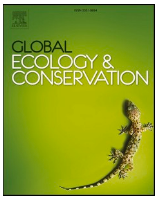

Dispersal success of a specialized tropical tree depends on complex interactions among diverse mammalian frugivores

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ABSTRACT

The study of seed dispersal in tropical forest communities is complicated by the high diversity of frugivores and the complex interactions among species and their environments. Determining which species are effective dispersers and which are opportunists with neutral or even negative effects on fruiting plants is a major problem which requires detailed studies focused on particular plant species. In this study we focused on seed dispersal of the wild rambutan (*Nephelium melliferum*) which supplies energy-rich fruits to primates and other mammals in a seasonal evergreen forest in central Thailand. We hypothesized that gibbons (*Hylobates lar*) were the most important dispersers and were capable of carrying and defecating seeds away from the tree crown where seeds or seedlings could escape increased distance or density-dependent mortality. We determined the seed dispersal effectiveness of all major arboreal consumers of *Nephelium* fruit (gibbons, pig-tail monkeys, squirrels) by using data on fruit production and consumption from fruit/seed traps under the canopies of eight sample trees, observations on animals feeding in fruiting trees, and seed deposition data at varying distances from tree crowns. We assessed the survival of seeds and seedlings in relation to distance from the crown by experiments and transect counts. Camera traps were used to detect consumption of seeds on the ground by terrestrial consumers. About half of the ripe fruit crop was harvested by squirrels which gnawed off the outer husk, ate the pulp and dropped intact seeds to the ground. Monkeys chewed and sucked off the pulp and dropped most seeds to the ground not far from the tree. Seeds and intact fruits dropped by squirrels and monkeys supported a large variety of terrestrial mammals most of which were seed predators. Gibbons, which swallow the seed with pulp attached, consumed only 16 % of the fruit crop but were the most effective and reliable seed dispersers overall, and appear to be the most specialized seed dispersal mutualist. Distance-dependent mortality was found in first-year seedlings, as well as evidence that further mortality must space out older saplings prior to recruitment into the tree population, which validates the importance of dispersal by gibbons. However, the great majority of fruits of *Nephelium melliferum* were consumed by mammalian opportunists and

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seed predators which interacted with one another in ways which depend on composition of the local community.

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1. Introduction

Seed dispersal is an essential ecological process in which fruit-eating animals play a major role, particularly in tropical rain forests (Jordano, 2000). The interactions that occur between these animals and the fruits they consume and potentially disperse are complex (Fedriani and Wiegand, 2014; Jordano et al., 2007; Levey and Benkman, 1999). The likelihood of a fruiting plant being visited by a suitable disperser can be influenced by aspects such as crop size and fruiting neighborhoods (Carlo and Morales, 2008; Herrera and Jordano, 1981; Morales et al., 2012), the density of frugivores (Stevenson et al., 2015), the nutritional needs and food preferences of the animals (Hodgkison et al., 2013, 2011), and the availability of alternative foods (Suwanvecho et al., 2018). Even aspects such as risk perception (Carreira et al., 2020) and personality (Zwolak and Sih, 2020) can influence foraging likelihood and dispersal outcomes. This complexity is compounded by the diverse feeding assemblages – including opportunists and predators – that often occur at fruiting plants which will vary locally and yearly, creating changing contexts, (Bronstein, 2001; Chamberlain et al., 2014; Fleming et al., 1993; Jordano et al., 2007; McConkey and Brockelman, 2011; Stoner et al., 2007; Suwanvecho et al., 2018). Such complexity makes it difficult to make generalizations or to determine exactly what species are the most effective dispersers of a given plant (Palmer et al., 2015; Howe, 2016). Overcoming such problems calls for detailed studies of fruiting plant species in varying local contexts, which may reasonably be possible for only a selected number of species, given the high diversity of tropical forest plants.

Seed dispersal research has advanced tremendously within recent decades, so that we have developed ways of assessing the contributions of various animals to the seed dispersal process (Jordano et al., 2007; Schupp et al., 2010), using this information to understand the network structure of seed dispersal communities (Bascompte and Jordano, 2007). Among the most important attributes of dispersers that we still need to understand at a community level is the extent of redundancy and complementary that exists among seed dispersers (McConkey and Brockelman, 2011; Rother et al., 2016; Schupp et al., 2010). Aside from the ecological knowledge such an understanding would provide us, it also allows us to assess the ecosystem consequences of declines in seed dispersers (Bueno et al., 2013). Redundant dispersers could theoretically be lost from an ecosystem with few consequences. Complementary dispersers provide altered roles and are probably required for long term survival of the plant population (McConkey and Brockelman, 2011). Accurate assignments of redundant and complementary dispersers must be based on a fine analysis of spatial and temporal aspects and relations between frugivore species. In addition, we must be able to recognize opportunistic frugivores that can have mixed effects on seed dispersal ranging between positive, neutral and negative (Bronstein, 2001; Howe, 2016; Loayza and Knight, 2010; Peña-Egaña et al., 2018).

The effectiveness of an animal species in dispersing seeds is indicated by the number of seeds handled (quantitative effectiveness) times the probability of a handled seed growing into a new plant (qualitative effectiveness) (Schupp et al., 2010). An animal identified as an effective seed disperser of a particular fruiting plant cannot be assumed to have the same effectiveness for other plant species. The complexity of seed dispersal systems means that the actual role will vary among consumed species. For example, gibbons (family Hylobatidae) are among the most effective mammalian seed dispersers, in a qualitative sense, in the evergreen forests of Southeast Asia (McConkey, 2009). Yet in six studies published on the seed dispersal ecology of food species common in their diet (Brodie et al., 2009; Hai et al., 2018; McConkey et al., 2014, 2015, 2018; McConkey and Brockelman, 2011), the role of gibbons varied somewhat. Gibbons tended to be good dispersers of seeds of protected fruits common in the diets of primates (Hai et al., 2018; McConkey et al., 2014, 2015) and deposited swallowed seeds away from tree crowns, but their importance was much less in the case of unprotected fruits which were shared with a variable suite of birds and other animals (McConkey and Brockelman, 2011). Gibbons often played a role complementary to macaques, the main primates that are sympatric with gibbons, and which are relatively inefficient dispersers. For one plant species macaques were responsible for more seedlings simply because of the larger numbers of seeds they moved (McConkey and Brockelman, 2011). In one study, barking deer (*Muntiacus muntjak*) were more important because deposition site was a crucial element of seed dispersal success and they deposited seeds in more favorable sites (Brodie et al., 2009). Such complex interactions that are exposed when plant species are the focus of detailed study have been found elsewhere as well (e.g., Wenny, 2000), highlighting a need for seed dispersal studies at both fine and broad scales if we are to accurately identify the roles of key seed dispersers.

Gibbons are generalist frugivores, feeding on a diverse range of fruit species (Marshall et al., 2009; McConkey, 2009; Suwanvecho et al., 2018). Our study species, *Nephelium melliferum*, despite having the characteristics of a specialized primate fruit with a protective husk (Fleming et al., 1993; Janson, 1983), is fed on by a diverse array of mammals, ranging from small squirrels to elephants (Kitamura et al., 2002). It is the most highly preferred fruit by gibbons during its fruiting season (Suwanvecho et al., 2018), and some of its congeneric relatives are economically important fruits (rambutans) that flood the markets when in season.

The husks of *Nephelium* fruits, and the habit of ripe fruits of remaining on the branches until picked, prevents virtually all frugivores from feeding on them (unless they are knocked off or dropped to the ground) except for arboreal mammals such as gibbons, which we have long known to be active consumers and potential seed dispersers. We therefore hypothesized that (1) the relationship between gibbons and our study species would support the asymmetric relationships identified in seed dispersal networks (Bascompte et al., 2006), so that the specialized plant would be dependent on a generalized disperser, while other consumers would be redundant or ineffective dispersers. We also hypothesized that (2) the gibbon–plant dispersal mutualism would be driven by post-dispersal consumption by seed or seedling predators, mostly terrestrial mammals, so that dispersal away from the crown avoids most density-dependent or distance-dependent mortality in seeds or seedlings, and that (3) heightened mortality of propagules would occur mostly under trees with large crops because of their greater capacity to attract seed and seedling predators. Because of the relatively small size of gibbon groups (average ca. 4 individuals) and their territoriality, however, gibbon proportional consumption should decline with large fruit crop size due to satiation.

2. Materials and methods

2.1. Study site

The study site is located in Khao Yai National Park, central Thailand (101°22' E, 14°26' N) in the 30-ha Mo Singto (MS) ForestGEO forest dynamics plot in the global network of the Center for Tropical Forest Science, Smithsonian Institution, Washington D. C. (Brockelman et al., 2017). The plot, located at 725–815 m altitude msl, lies in seasonal evergreen forest that receives 1200–3000 mm of rainfall per year (average 2073 mm over 21 years; Brockelman et al., 2017, National Park Division data), mostly during May–September. The dry season usually lasts from late October to April. The MS plot was surveyed into 20 m × 20 m squares and all trees $\geq$ 10 mm in diameter at breast height (dbh) at 1.3 m height from ground were mapped, tagged, and identified in 2001, and at subsequent 5-year intervals since. Maximum fruit availability at the study site occurs from April to June (Brockelman, 2011). Interannual variation in fruiting is widespread on the plot (Brockelman et al., 2014) and is largely unsynchronized between species, so that frugivores must switch foods from year to year (Suwanvecho et al., 2018).

Khao Yai National Park (2168 km^2) supports a diverse bird (*c*. 320 species) and large mammal fauna (at least 71 species) (Lynam et al., 2006). The gibbon (*Hylobates lar*) population exists at high density with about 4 groups (about 16 individuals) km^{-2} (Brockelman, 2004; Brockelman et al., 1998). The main gibbon study group (Group A; 4 members at the time of study) had a home range of 27 ha and occupied about 80 % of the 30.5-ha plot. The other primate species present, the pig-tailed macaque (*Macaca leonina*), occupied much larger ranges (1–7 km^2; T. Savini, pers. comm.) and entered the plot occasionally in large groups of over 50 individuals. The group overlapping the study area had a home range of 4.5 km^2 (José-Domínguez et al., 2015).

Other mammalian frugivores inhabiting the study site include sambar deer *Rusa unicolor*, red muntjac (barking deer) *Muntiacus muntjak*, Asian elephant *Elephas maximus*, wild pig *Sus scrofa*, Himalayan black bear *Ursus thibetanus*, sun bear *Ursus malayanus*, and several species of civets. Three species of canopy squirrels consume *N. melliferum* fruits: black giant squirrel *Ratufa bicolor*, variable squirrel *Callosciurus finlaysonii* and Himalayan striped squirrel *Tamiops mcclellendii*.

2.2. Study species

Nephelium melliferum Gagnep. (Sapindaceae) is a common tree of the seasonal evergreen forest in Khao Yai National Park and plays a vital role in the food economy of the forest for mammals, especially primates. The species begins reproduction at an average of ca. 20 cm in dbh and reaches a maximum size of over 70 cm. There are nearly 300 trees of reproductive size, for a density of about 10 trees ha^{-1} on the Mo Singto plot. A minority of these bear fruit in any given year, however, and 40% of trees have reached the size of 30 cm or more in dbh without having produced any fruit in at least eight years of monitoring (unpublished data). Mast fruiting episodes (when more than half the trees have fruit) occur every 3–6 years. We studied the species in 2004 and 2007 (both mast fruiting episodes when nearly 70 % of trees produced fruit).

Fruits of *N. melliferum* are drupe-like, generally ellipsoid in shape, with an average length of 34 mm (range 20–43 mm) and a single seed of c. 20 × 12 × 11 mm. The outer inedible rind of the fruit is covered with large soft spines and turns from light green to bright red when ripe. The white pulp is soft, sweet-sour, and moist.

Table 1
Overview of methods used to study seed dispersal of *Nephelium melliferum*.

Seed dispersal stage	Method used	Sample size	Year studied
Frugivory – arboreal (estimates of crop size)	Fruit & seed traps	8 trees	2004
	Tree watches	5 trees, 103 h	2004
Frugivory – terrestrial	Camera-traps	2 trees 5 trees 10 trees	2004 2018–19 2020, 2022
	Opportunistic methods – feeding fruit to habituated animals (sambar deer, muntjac), searches for dung (elephant, bear)		2004–2019
	Marked & monitored seeds	6 trees	2007, 2019
Seed dispersal distances (estimates of crop size)	Transects (macaques, squirrels)	7 trees	2004, 2007
	Gibbon follows	97 feces	2007
Seed fate & germination	Experiment	5 trees	2004, 2007
Seedling survival (1 y)	Transects	9 trees	2007, 2008

2.3. Data collection

2.3.1. General overview

We collected data on five stages of the seed dispersal process for *N. melliferum* and used multiple methods to measure these (Table 1). We aimed to document each dispersal stage as well as determine the overall contribution of the main seed dispersers of *N. melliferum* using the Seed Dispersal Effectiveness (SDE) framework (Schupp et al., 2010). The five main stages were: (1) frugivory by arboreal animals, (2) frugivory and seed predation by terrestrial animals, (3) seed dispersal distances, (4) seed fate and germination and (5) seedling survival. Fruit crop sizes were also estimated for sampled trees to allow comparison with arboreal and terrestrial fruit consumption. The intermittent fruiting phenology of the species resulted in data collection being spread from 2004 to 2019; we sampled frugivory in the heavy fruiting years of 2004 and 2007, and were unable to follow-up this sampling with seed predation work until the poorer fruiting seasons of 2018 and 2019. A final planned sampling period of 2020 was prevented by restrictions on entry to the park caused by covid-19.

2.3.2. Frugivory by arboreal animals: Fruit and seed traps

Eight trees were selected for monitoring with fruit traps, from a total of 263 trees that were within the range of the gibbon study group and were over 20 cm dbh in 2004. The eight trees were selected randomly from a list of 22 trees known to have fruited reasonably heavily at least once over the past five years, and which were not covered with woody vines (which suppress fruit production and also make observation difficult). Ten traps were placed in a random pattern below the canopy of each of the studied trees before the fruit was ripe. Traps were 0.5 m^2 in area and consisted of plastic window screen bags sewn onto heavy wire circular loops supported ca. 1 m above the ground on stakes. Fallen fruits, seeds and remains of husks were collected from the traps every two days until less than three fruit were found in the combined traps (a total of 24–34 days of monitoring for each tree). These data were used to determine the overall crop size and the quantity of fruit consumed by different animal species. Five categories of fruit were distinguished in the traps: unripe intact fruit, ripe whole fruit, husked fruits and seeds sucked by macaques (clean and smooth), seeds with the pulp chewed off by squirrels (evident from tooth marks), and husks removed and dropped by gibbons. The three squirrel consumers could be distinguished by the relative sizes of their tooth impressions on the seed surface. Feeding by gibbons (which swallow seeds and pulp) could be recognized by the presence of husks sliced into two neat halves, which they dropped directly below the canopy. Gibbons consumed all fruits where they picked them; they did not carry fruits away from the canopy before consumption. Both macaques and squirrels dropped husks cut into irregular fragments. Seeds dropped by squirrels had all flesh gnawed off, but those dropped by monkeys usually retained some pulp and lacked tooth marks. Feeding signs by different animals were confirmed by direct observations matched with dropped fruit and seeds during tree watches (next section). The relative contributions of macaques and gibbons to the dropped husks were checked against information obtained during the tree watches; this was done to determine if macaques were swallowing seeds and, therefore, the empty husks being mistakenly associated with dropped seeds.

Pteropodid bats in the genus *Cynopterus* are known to consume *Nephelium* fruit (Tan et al., 2000) and are present in the study site, but we found no characteristic signs of bat feeding (i.e., feeding roosts) during the study and assumed their role in dispersal to be minimal.

2.3.3. Frugivory by arboreal animals: Tree watches

Over 9 days, 103 h of observations were completed on five trees bearing ripe fruit. Observations were spread uniformly between dawn and dusk. The entry and exit times, group size and feeding rate were recorded for each feeding event. Feeding behavior was also observed (i.e., whether the fruit was removed and swallowed, spat or dropped) and we confirmed that the feeding sign left on dropped fruit and seeds matched that assigned in the fruit traps.

2.3.4. Frugivory by terrestrial animals

Frugivory by terrestrial animals was studied primarily using camera traps. In 2004, two infrared-beam camera traps (Camtrakker™, Camtrak South Inc., Georgia, USA) were set up near two trees (10 days under each tree, taking photos only). These data were used to identify consumers). In 2018 we placed single camera-traps under each of four trees found to be fruiting, and one camera-trap under a single fruiting tree in 2019, for a total of 65 camera-trap days. The cameras (Chinese models made for the Chinese Academy of Sciences) under these five trees were set to record video. From these cameras we recorded visit frequency and foraging behavior of terrestrial animals. The year 2020 was also a poor fruiting year, but we managed to install camera traps (Chinese models) under five fruiting trees. These were aimed toward the ground more than in previous attempts, in order to record visits by more small mammals which may be consuming seeds.

We also confirmed seed handling of terrestrial consumers using opportunistic finds of feces (bear, elephant) and by feeding sign on seeds monitored under the crown (rats). To determine the fate of *N. melliferum* seeds consumed by barking and sambar deer, we fed fruit and seeds to habituated wild animals that forage around human-used areas and recorded their handling behavior; both deer species chewed up seeds and fruits and we classified them as seed predators.

To determine what proportion of fruit and seeds were removed by terrestrial consumers under the tree crown, and to provide comparative estimates of crop sizes, we counted and monitored naturally-fallen or dropped (by macaques or squirrels) fruits and seeds along transects. These were done in 2007 ($n = 5$ trees; transects and fruit or seed removal) and 2019 ($n = 1$ tree; no more fruiting trees could be located in this year; seed removal only). In 2007, 20 seeds and 20 fruits were marked individually under the crown of each of 5 trees ($n = 100$ seeds and 100 fruits across all 5 trees) using a wooden chopstick and small piece of flagging tape. Seeds and fruits fallen naturally in 2-m wide transects, radiating from the tree trunk to the edge of the canopy ($n = 4$ transects running in the cardinal directions) were counted (providing estimates of relative crop size) and monitored. We also monitored the fate of seeds placed 5 m and 10 m from the crown edge on extensions of these four transects (20 seeds at each distance category, with five seeds at each location). The fate of the seeds and fruits was monitored daily for 10 days and then at 2 months (encompassing the fast germination period for this species). Our estimates of seed and fruit removal by terrestrial animals are based on the number of germinated seedlings after 2 months. In 2019, we monitored 100 seeds placed in groups of 5 spaced out under the single tree for 2 weeks (until fruiting had almost ceased).

2.3.5. *Seed dispersal distances*

The ranging behavior of gibbon group A was determined by following the group for 6 days each month during 2003–2005, and for 30 days each month during the fruiting season from 2006 to 2011 (Suwanvecho et al., 2018). During the latter 6 years *N. melliferum* fruited heavily only in 2007, and less heavily in 2011. On a typical follow, three observers would locate the group at its sleeping tree at dawn, when the group would defecate and enter a nearby *N. melliferum* tree for its first meal. The observers who followed the group recorded the tag numbers of all trees entered and food species eaten by the two adults, and also collected all feces defecated by the gibbons and counted the seeds of all fruit species defecated. Dispersal distances for *N. melliferum* seeds defecated by gibbons were measured using the *x*-*y* co-ordinates of trees (from the plot census database) below which seeds were defecated and those of the nearest fruiting *N. melliferum* trees. For seeds dispersed by the zoochorous gibbons, the nearest fruiting tree was not likely to be the parent tree of origin. Therefore the distance to the nearest fruiting tree gives only a minimum estimate of the dispersal distance from the tree of origin, because the gibbons usually fed in more than one *N. melliferum* tree over the course of the day. For the purpose of studying distance and density-dependent effects on seed survival, however, the distance to the nearest fruiting tree is more relevant than distance to the parent tree which may be hundreds of meters away at the time of seed defecation.

Dispersal distances for macaques (which spit most seeds) and squirrels (which drop seeds), were measured using transects extending away from fruiting trees. Because dispersal distances of these mammals were short, it was assumed that the nearest fruiting tree was the tree of origin. Four 2-m-wide transects, radiating north, south, east and west from the tree base to 40 m beyond the tree crown, were established under three trees in 2004 and five trees in 2007 and monitored for seven days. Transects were walked daily and all seeds and fruit found were recorded and removed. Handling methods for seeds and fruit were distinguished using the same criteria as for fruit caught in traps. Counts were converted to number of seeds day^{-1} tree^{-1} and their density (m^{-2}), for the crown area and at 10-m intervals from the crown edge.

These seed and fruit counts from the 2007 data ($n = 5$ trees) were used to estimate relative crop sizes in relation to seed removal by terrestrial animals (described in the previous section). We did not combine the 2004 and 2007 data for this test to avoid the effects of other influences (i.e., different sets of fruit tree species available) on feeding patterns.

2.3.6. *Seed fate and germination*

Experiments were done in situ to test the effects of seed handling by frugivores and distance to *N. meliferum* trees on seed survival in 2004. The experiments were carried out around 5 randomly selected *N. melliferum* trees > 40 cm in dbh. The following treatments were carried out: (i) dispersal agent: cleaned seeds dropped by squirrels or monkeys (gibbon-dispersed seeds were not available for this experiment); (ii) distance: under canopy, 5 m beyond edge of canopy and 30 m beyond edge of canopy (primate-handled seeds only as squirrels did not disperse seeds to this distance); (iii) predator exclusion: seeds in open and seeds enclosed in small cages with 1-cm wire mesh 6 × 6 × 4 cm in dimensions. Ten seeds of each treatment were placed in cages or individually placed (>50 cm apart) under or near each tree at randomly selected locations. Seeds were monitored daily for the first week, weekly for one month and then monthly for 5 months, to record seed removal, germination, and seedling establishment.

2.3.7. *Seedling survival*

Six weeks after fruiting finished in 2007, we recorded and mapped *N. melliferum* seedlings along transects radiating from 10 study trees. There is no dormancy in this species and seeds germinate 4–15 (median ca. 9) days after falling to the ground under moist conditions. Four transects were established from the tree base to 40 m in the four cardinal directions; transects were 1 m wide for the first 15 m and 2 m wide for the remaining distance. These transects were repeated in September 2008, to record seedling survival over 1 year.

2.3.8. *Effectiveness of seed dispersers*

We calculated the overall seed dispersal effectiveness (SDE) of the different frugivores by determining their quantitative and qualitative contributions, and displaying this on a SDE landscape (Schupp et al., 2010; Schupp, 1993). The quantitative contribution is defined as the probability of a seed being removed by that animal (i.e., the proportion of the crop consumed). The qualitative component was defined as the probability of a handled seed producing a 1-y-old seedling. Probabilities were calculated by multiplying the distance-dependent survival factors at each stage of recruitment (germination, 1-y seedling survival) with the proportion of seeds dispersed to each distance category by each disperser. We also compared SDE values for animals and trees with large vs. small crops, using the data collected during the study.

2.4. *Data analyses*

To estimate total crop size, we used the numbers of whole fruit and husks that fell into the seed traps, and extrapolated these values to the entire canopy area under each study tree. The data from the seed fate experiment were analyzed using two-way ANOVA.

Correlations between crop sizes and consumption variables were made using Pearson's correlation coefficient. Statistical analyses were performed in R (R Core Team, 2021). The SDE landscape figure was produced in Excel.

3. Results

3.1. *Frugivory by arboreal animals*

The total ripe fruit crop of the eight study trees varied from ca. 3000–24,000 fruits (Appendix B2), and the percentage consumed by the different arboreal consumers varied between trees (Appendix B3). Some of this variation was related to crop size (reported below).

Nearly half the fruit caught in the traps had been cleaned of pulp and the seeds dropped by variable squirrels, *Callosciurus finlaysonii* (47.9 ± 20.9 %, mean ± 1 standard deviation across eight sampled trees; Appendices A and B3; Fig. 1). Gibbons consumed 16.3 ± 12.8 % of the fruit crop, and macaques 12.6 ± 12.2 %. Giant squirrels, *Ratufa bicolor,* consumed few fruit (1.3 ± 1.2 %). We recorded the small squirrel, *Tamiops macclellandii,* during the tree watches but they were present only 1 % of the overall time frugivores were present in the five trees (Appendix A) and we did not record their dropped seeds in the traps. In total, based on fruit traps, arboreal consumers consumed an average of 78.3 ± 13.5 % of the available crop per tree.

Intact fruit represented 6.2–51.1 % (average = 21.7 %) of the *N. melliferum* diaspores found in fruit traps under each tree. We found significantly more intact fruits in traps under trees where macaques ($r = 0.869$, $p = 0.004$) and *C. finlaysonii* ($r = 0.78$, $p = 0.022$) fed most, suggesting these animals were responsible for dropping fruits in addition to handling seeds (Appendix B). We also found small quantities of bitten seeds in the traps, indicating that some consumers (most likely macaques) were occasional seed predators.

3.2. *Frugivory by terrestrial animals*

Ten mammal species were recorded consuming *N. melliferum* fruit from the ground, based on camera traps, feeding tests and tree watches (Appendix A). This includes macaques which consumed fruit on the ground as well as in the canopy. In the camera traps we recorded a total of 311 visits by animals known to consume the fruits or seeds of *N. melliferum*. Only three of the ground-feeding species were confirmed to disperse undamaged seeds: elephants *Elephas maximus* (4 visits, seeds also found in dung), sun bear *Helarctos malayanus* (2 visits) Asiatic black bear *Ursus thibetanus* (1 visit) (bears recorded by cameras and seeds found in dung), and macaques (61 visits) (Fig. 1). At least five taxa destroyed the seeds (Fig. 1, Appendix A). The most common seed predators were barking deer *Muntiacus muntjak* (107 visits) and sambar deer *Rusa unicolor* (65 visits), while wild boar *Sus scrofa* (6 visits), porcupine *Hystrix brachyura* (3 visits) and rats (in 2004 and 2020) were also recorded. For these animals, predation was confirmed by feeding tests with habituated animals (sambar and barking deer), by observations in the camera-trap videos (boar, porcupines and rats) or by observed damage on the seed (rats). Rats (*Maxomys surifer* and possibly other species) were recorded (54 visits to five trees) in 2020 when cameras were aimed at the ground. Rats could be secondary dispersers as well as predators of seeds. We do not know the fate of seeds consumed by three terrestrial bird species recorded in 2004 (Siamese fireback *Lophura diardi*, silver pheasant *Lophura nycthemera*, white-crowned laughing thrush *Garrulax leucolophus*), and lesser mousedeer *Tragulus javanicus* (1 visit). We found one bear feces (bear species unknown) with *N. melliferum* seeds and recorded each bear species once in camera-trap videos, although they were observed

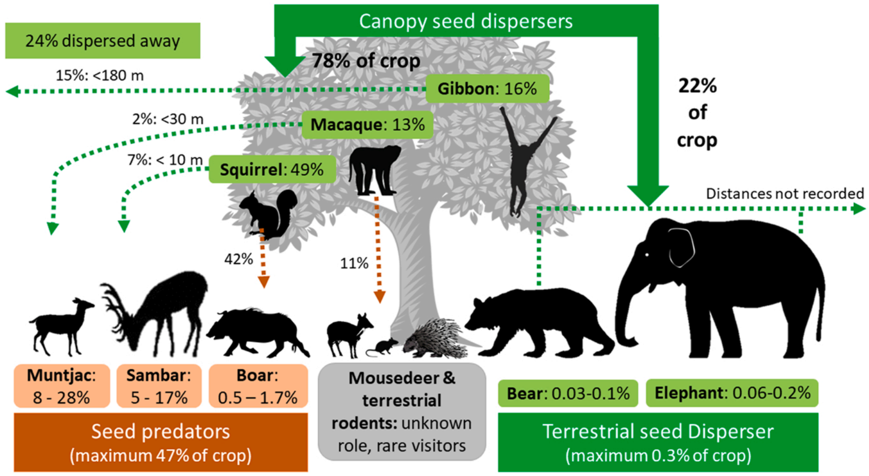

Fig. 1. The complex seed dispersal system of *Nephelium melliferum*. The average tree percentages of the total ripe tree crop (Appendix B3) are shown for each category of consumer. Where a range of values is given, it represents the variability across trees. Most of the crop is consumed by arboreal frugivores, and all these species except for gibbons drop most seeds on the ground under or near the trees where they are consumed by a variety of terrestrial seed predators, and by bears and elephants which are potential seed dispersers. Bears are partly terrestrial and partly arboreal frugivores, but although their claw-marks appeared on several species of fruiting trees, we were never able to watch them eating fruit.

only sniffing fruit on the ground.

3.3. *Variation in fruit consumption among trees and the effect of crop size*

The total number of ripe fruits available to arboreal frugivores (based on the fruit traps) ranged from 3017 to 24,253 fruits per tree (mean ± SD, 11,537 ± 7253; Appendix B2). The quantity of fruit consumed by *Callosciurus finlaysonii* was strongly related to crop size ($r = 0.956$, $p = 0.0002$); consumption was more weakly related to crop size in gibbons ($r = 0.687$, $p = 0.059$; Fig. 2A) and *Ratufa bicolor* ($r = 0.697$, $p = 0.054$). The quantity of fruit consumed by macaques was not significantly related to crop size ($r = 0.560$, $p = 0.148$). However, the percentage of the crop consumed in relation to crop size was positive for gibbons ($r = 0.371$, $p = 0.366$) and negative for macaques ($r = -0.561$, $p = 0.149$), but in neither case significant. For *C. finlaysonii* and *R. bicolor*, percentage consumption in relation to crop size was also nonsignificant (*C. finlaysonii,* $r = 0.458$, $p = 0.253$; *R. bicolor*, $r = 0.267$, $p = 0.522$). In the case of gibbons, total consumption and percentage consumption were markedly lower for the most productive tree (Appendix B, Fig. 2B), even though it was the most favored food source, reflecting the limited capacity of a single territorial group to consume all available fruits.

Among arboreal consumers, the only significant interactions that occurred were between squirrels *C. finlaysonii* and macaques. The squirrels tended to avoid trees occupied by large numbers of macaques but were not much affected by gibbons feeding in the tree. The percentages of fruit consumed by squirrels and macaques were negatively related ($r = -0.87$, $p < 0.01$; Appendix B). Gibbon percentage consumption had a weak negative correlation ($p = -0.458$) with the percentage consumption by macaques, as gibbons could not withstand aggression by large numbers of macaques. In several instances, we saw gibbons temporarily leave the tree when a large monkey group arrived.

The three main arboreal consumers showed different temporal patterns of feeding, when daily feeding rate is related to the abundance of fruit available each day across all trees (Fig. 3). The number of fruits consumed by gibbons each day was the best match for daily availability ($r = 0.936$, $p < 0.0001$). Macaques consumed few fruits per day until *N. melliferum* reached its peak availability ($r = 0.823$, $p < 0.00001$), which suggests that feeding by large groups of macaques is constrained by patch (tree crop) size. The very

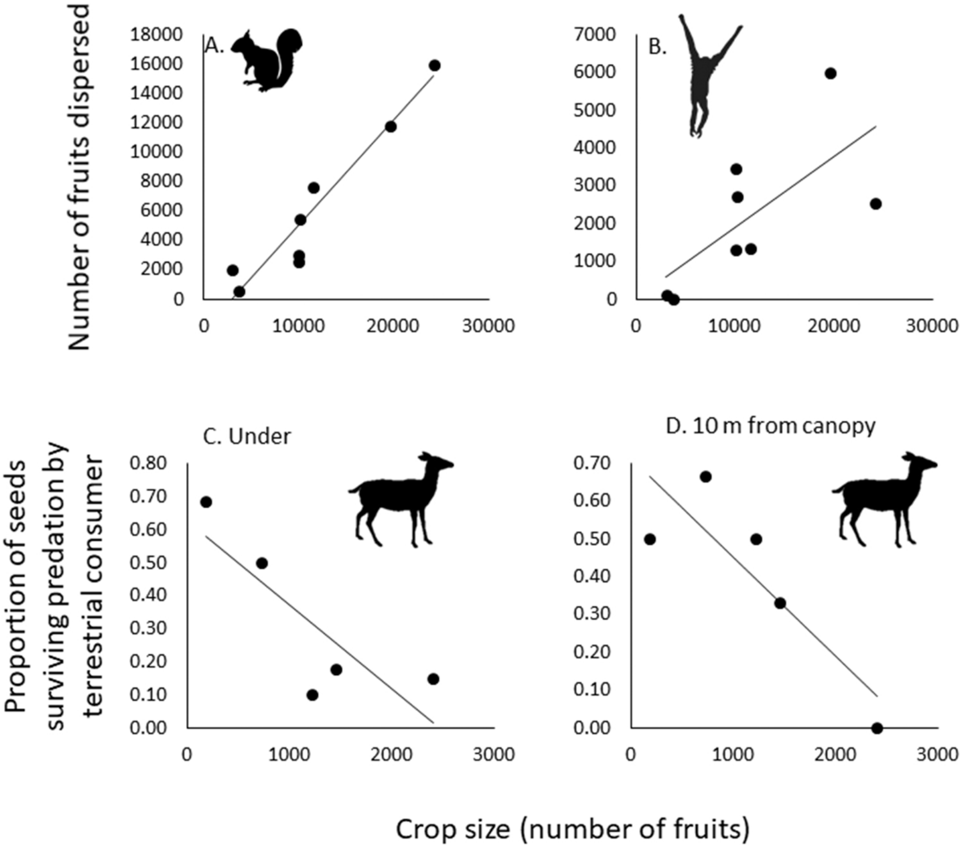

Fig. 2. Relationship between crop size and fruit consumption for (A) *Callosciurus finlaysonii*, and (B), gibbons (see text). The relationship between *Ratufa bicolor* (squirrel) and crop size was weakly significant but is not displayed here since they were infrequent consumers. Panels C and D show the numbers of seeds surviving consumption by terrestrial seed predators under the tree crown and at 10 m from the tree crown, respectively, for five trees studied in 2007.

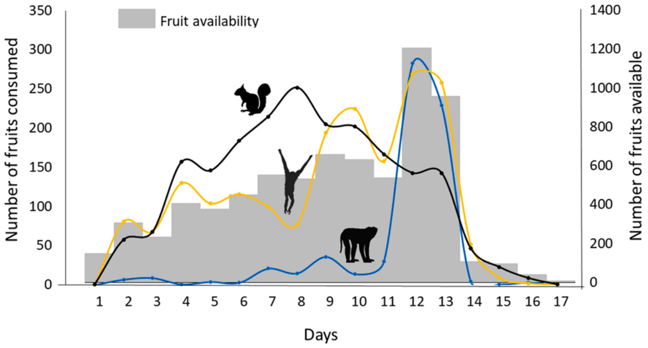

Fig. 3. Consumption of *N. melliferum* fruit by squirrels, gibbons, and macaques across days, in relation to the daily availability of fruit ($n = 8$ trees).

common squirrel *C. finlaysonii* consumed the most fruit before the peak in abundance although the relationship with fruit availability was still significant ($r = 0.680$, $p = 0.002$). Fruit consumption by *C. finlaysonii*, however, was most closely correlated with tree crop size (Fig. 2A), which suggests that food was more limiting to this species than to other species, and that patch size was not a factor in the selection of trees by squirrels.

Removal of intact fruit from the ground by terrestrial feeders ranged from 10 % to 45 % of that available ($n = 5$ trees, with 100 fruit in total, mean ± SD = 21.7 ± 12.1 %), while removal of dropped seeds ranged from 5 % to 73 % ($n = 6$ trees in 2007 and 2019, 200 seeds in total, mean = 19 ± 26 %). In 2007, counts of uneaten fruits and seeds dropped along the transects under the tree crowns ranged from 183 to 2401 ($n = 5$ trees). The probability of seeds under the crown surviving to germination (2-month check) was negatively related to crop size ($r = -0.877$, $p = 0.051$, $n = 5$ trees) (Fig. 2C), ranging from 10 % to 15 % in the trees with the largest crops to 69% in the tree with the smallest crop; this suggests seed predators targeted trees with large crops. The correlation between proportion of seeds surviving to germination and crop size was not significant at 5 m from the tree crown edge ($r = 0.385$, $p = 0.52$), but was close to significance 10 m from the crown edge ($r = -0.865$, $p = 0.058$; Fig. 2D), suggesting foraging animals were also likely to consume seeds dropped close to the crown edge. The proportion of intact fruit surviving was not related to crop size ($r = -0.51$,

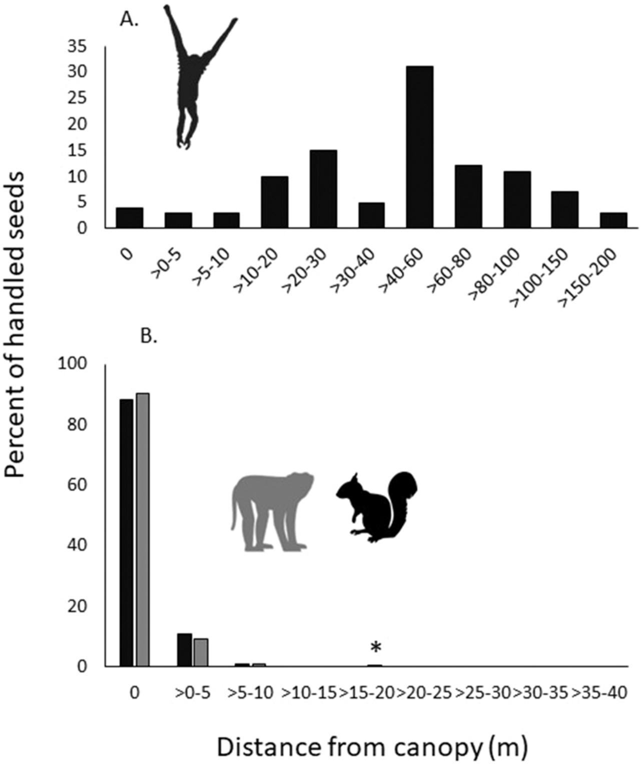

Fig. 4. Dispersal distances of *N. melliferum* by (A) gibbons and (B) squirrels (black) and macaques (gray). The *x*-axis has a different scale in each graph, and "* " highlights the few seeds dispersed by macaques to this distance.

$p = 0.38$).

3.4. Seed dispersal distances

Gibbons were the frugivores most likely to disperse seeds away from parent crowns, with 4 % of seeds defecated under fruiting *N. melliferum* trees in 2004 (from gibbon-follow data), and the remainder dispersed up to 161 m away (Fig. 4a). These data underestimate the total dispersal distance by gibbons because the actual trees in which the seeds were obtained are not known, and several *N. melliferum* trees were typically fed in each day (Suwanvecho et al., 2018). Gibbons commonly travel two to three times the width of their territory each day while foraging and defending it against intruders (Bartlett, 2009), and most seeds defecated under a tree are not likely to have been consumed from that tree. Macaques spat 86 % of handled seeds under the crown, with 10 % spat within 10 m of the crown and the remainder at distances of up to 30 m (data from seven trees with transects in 2004, 2007). Additional macaque-spat seeds (not on monitored transects) were found up to 30 m away from adult *N. melliferum* trees. Squirrels dropped most seeds under the crown (85 %), with the other 15 % of seeds dropped within 10 m from fruiting crowns (Fig. 4).

One bear scat containing 230 *N. melliferum* seeds was found 30 m from the nearest fruiting *Nephelium* tree in 2004. Three *N. melliferum* seeds were also recovered from one elephant dung in 2009 (of 49 dung piles checked for seeds). Two of these seeds were viable and one was broken into two pieces.

3.5. Seed fate

In the seed survival experiments (2004), there was no difference in seed fate between fallen whole fruits and those handled by primates and squirrels, either in cages or outside ($F = 0.72$. $p = 0.498$) (Table 2). However, seeds in the predator-exclusion cages survived to 5 months at a significantly higher rate than seeds in the open, under the crowns of the trees (40 % vs. 4.0 % for primate seeds, 58 % vs. 6.0 % for squirrel seeds; $F = 50.98$, $p < 0.001$). This indicates that mammals (rodents or deer) were likely to have been the major predators, and insects and other sources of mortality (e.g., fungi) destroyed few or no seeds. For non-caged seeds, those placed 5 m away from the canopy survived at a higher rate (32 % for primate seeds and 40 % for squirrel seeds) than those placed under the canopy (5 % of both species combined) ($F = 12.20$, $p = 0.003$). None of the 230 *N. melliferum* seeds in the bear dung produced seedlings, although some seeds germinated initially. The two intact seeds from elephant dung germinated and established seedlings.

3.6. Seedling survival

In 2007, seedlings occurred at 83 times higher density shortly after germination under the 10 study trees (mean ± SD: 12.47 ± 7.94 seedlings m^{-2}, range 4.45–30.23) than in the region from the tree crown edge to 30 m (0.15 ± 0.08 seedlings m^{-2}, range 0.03–0.29) (Fig. 5A). After one year, the disparity was reduced to 53 times higher density under the crown (3.15 ± 2.69 seedlings m^{-2}, range 0.74–8.95) than away from the crown (0.06 ± 0.04 seedlings m^{-2}, range 0.02–0.15). Only nine trees were sampled in 2008, because one tree had fallen. There was evidence of positive distance-dependent seedling survival in seven out of the nine trees (mean ± SD proportion surviving, under 0.25 ± 0.013, away 0.39 ± 0.19; paired t-test across all nine trees, $t = 2.26$, p (one-tailed) $= 0.027$) (Fig. 5B). Survival was not related to seedling density under the crown ($r = 0.050$, $p = 0.89$), or away from the crown ($r = 0.032$, $p = 0.934$).

3.7. Relative effectiveness of frugivores

The most effective dispersers of *N. melliferum* were gibbons (SDE = 0.019, using average values across all study trees), which were responsible for 54 % of seedlings surviving to one year (Fig. 6). *C. finlaysonii* squirrels were also effective dispersers (SDE = 0.013), producing 37 % of 1-year-old seedlings, although all of these germinated within 10 m of the parent tree crown. Hence, later distance-dependent mortality would disproportionately reduce this contribution. Macaques were not effective dispersers (SDE = 0.003, 8.7 % of

Table 2
Survival of *N. melliferum* seeds to germination under different treatments. Seeds were caged or left open (not caged), were handled by primates or squirrels, or left whole, and were placed at different distances from the crown edge. The distances reflected the respective handling behavior of different animals, and, hence the treatment of squirrels at 30 m was not tested. Values shown at the mean number of seedlings (out of 10 seeds per treatment) and the standard error. The cage and distance treatments produced significant results, but not the dispersal agent.

Treatment	Dispersers		
	Primates	Squirrels	Intact fruit
Cage	4.0 ± 1.30	5.8 ± 1.77	6.8 ± 1.36
No cage	0.4 ± 0.24	0.6 ± 0.40	0
Under	0.4 ± 0.24	0.6 ± 0.40	
5 m from canopy edge	3.2 ± 1.28	4.0 ± 0.89	
30 m from canopy edge	2.8 ± 0.80	Not tested	

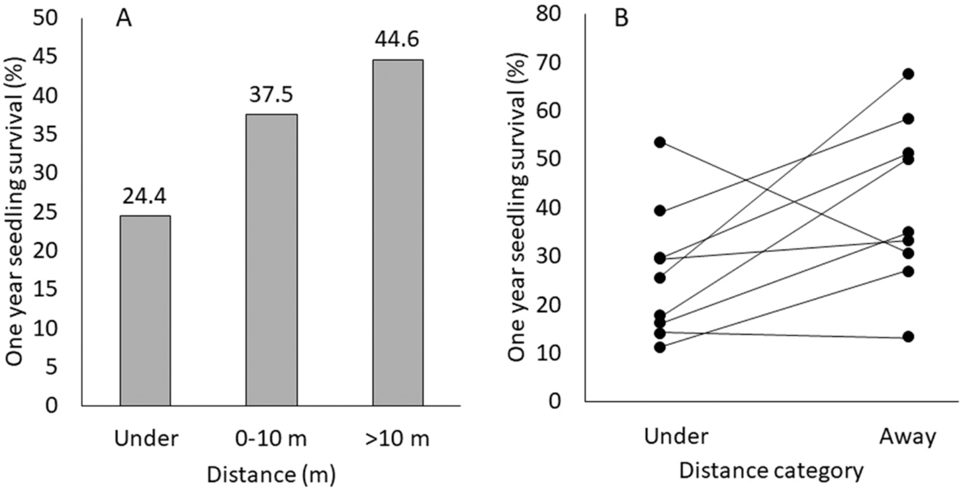

Fig. 5. Survival of *N. melliferum* seedlings in 2007 from soon after germination to one year for nine trees. A, Survival of all seedlings combined under, just beyond, and > 10 m beyond the crowns. B, One-year survival of seedlings under the crown and beyond the crown (up to 30 m) for each of the nine trees separately.

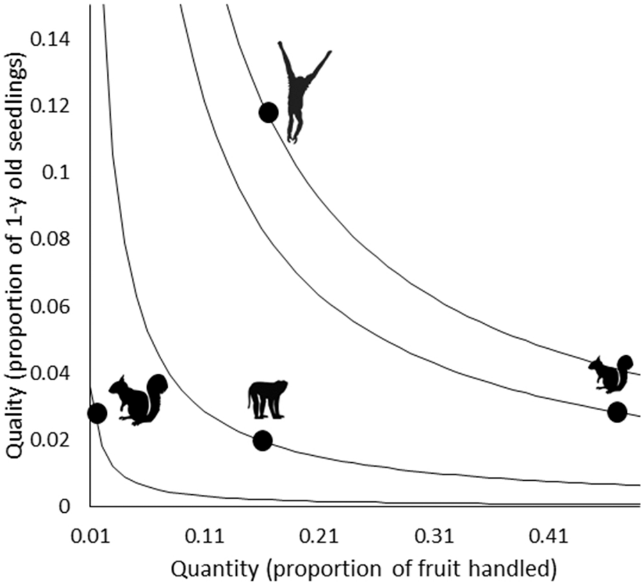

Fig. 6. Seed Dispersal Effectiveness (SDE) of the four consumers of the fruit of *N. melliferum.* The isoclines mark loci of equal effectiveness. Gibbons have the highest effectiveness followed by *C. finlaysonii* (small squirrel on right), macaques and *R. bicolor* (large squirrel). Values are based on averages across all study trees.

seedlings), nor were the large but less common *R. bicolor* squirrels (SDE = 0.0004, 1 % of seedlings).

When we calculate SDE according to the different rates of seed removal (predation) in the trees with the largest and smallest crops, then gibbons are disproportionately important for seed dispersal from large crops (SDE = 0.018, 89 % of seedlings, with 8 % by *C. finlaysonii*) (Fig. 7), while *C. finlaysonii* had the highest SDE for small crops (SDE = 0.025, 48 % of seedlings, with 39 % by gibbons).

4. Discussion

At least 15 species of mammals, both arboreal and terrestrial, consumed either seeds or fruit pulp of the tree *Nephelium melliferum.* This study has attempted to determine how each species is involved in the dispersal success of the tree, and the role of each species. No two frugivore species had the same effect on the seed dispersal process. Species differed in the quantity and quality of dispersal, distances seeds were carried, and foraging behaviors such as times of visits, and numbers of trees visited, and whether visits were influenced by crop size. Several types of interactions between species occurred, rendering the role of particular species in dispersal

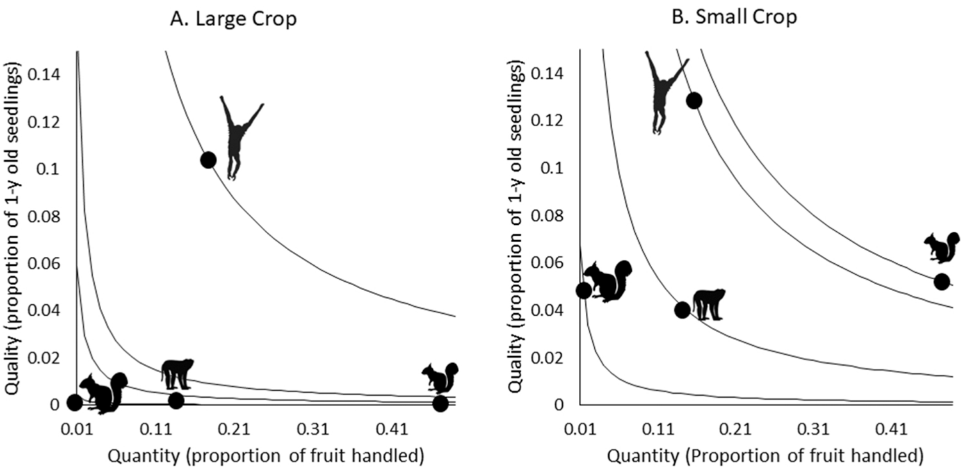

Fig. 7. Seed Dispersal Effectiveness (SDE) of the four consumers of the fruit of *N. melliferum* for (A) three trees with medium to large crops and (B) two trees with smaller crops. Gibbons were the only effective disperser in trees with large crops, while *C. finlaysonii* (small squirrel) was the most effective for small crops, albeit closely followed by gibbons.

dependent on local context (Thompson, 1988, 2005; Perea et al., 2013; Palmer et al., 2015; Suwanvecho et al., 2018). Overall, gibbons appeared to be the most effective of the dispersers, although they did not handle the most fruits. Unlike squirrels and monkeys, they dropped relatively few fruits. Seeds were carried beyond the tree crown and defecated some distance away, up to the width of the home range which for group A is roughly 500 m. The relative dispersal effectiveness of gibbons depended in part on the amount of fruit and seeds dropped by monkeys and squirrels. Interactions between monkeys and squirrels was somewhat unpredictable, but squirrel consumption in some trees was less when monkeys fed more, possibly being suppressed by monkey presence and aggression. We observed squirrels leaving trees as monkeys arrived, perhaps to avoid predation (Sushma and Singh, 2008). Visits by large groups of monkeys at trees were somewhat fortuitous and unpredictable. Wild elephants and bears had a relatively minor, and also very unpredictable, effect on seed dispersal success but, unlike deer, they were both potential long-distance dispersers rather than predators (Campos-Arceiz and Blake, 2011; Naoe et al., 2016). The relatively minor role of elephants and bears in *N. melliferum* seed dispersal could be attributed to low population densities due to human exploitation; however, both elephant and bear signs are widespread throughout the park, and elephant poaching has not been a problem in Khao Yai. We believe that their relatively small role in seed dispersal is due to their broader diets, and more sporadic occurrence at fruiting trees. We may also have underestimated their roles by concentrating mainly on arboreal mammals, and more intensive study of the roles of large terrestrial mammals is due.

The major requirement of the Janzen–Connell hypothesis regarding biodiversity regulation of propagules is con-specific density- or distance-dependent survival of seeds or seedlings (Terborgh, 2020). Predation and disease are regarded as dominant forces affecting species diversity in tropical forests (Terborgh et al., 1993; Terborgh, 2020). Predation by generalist herbivores such as deer, however, is not highly species-specific and may not contribute much to maintenance of species diversity (Hammond and Brown, 1996; Janzen, 1970; Terborgh, 2020). Distance-dependent predation on seeds and seedlings of *N. melliferum* was provided mainly by deer at the Mo Singto site but was relatively weak. Insect predation played little or no role, as deer and other terrestrial foragers usually consume fallen fruits and the soft, unprotected seeds before any insect can complete its life cycle inside a seed. We have found that seed predation rates in relation to distance are difficult to measure and results are not always consistent with Janzen–Connell, due in part to the variable amounts of uneaten fruits and seeds falling and variation among trees in crop size. An earlier study carried out by Vimuktayon (2001) just after the Mo Singto plot was surveyed followed the survival of 1847 *N. melliferum* seeds defecated by the gibbons in situ. Most of these seeds (63 %) disappeared within one month, but 8.9 % survived as seedlings after one year and 6.2 % after two years. Average dispersal distance from the most productive tree was estimated as 153 m ($n = 209$ seeds) and ranged up to 320 m. Vimuktayon (2001) estimated the survival of seeds dropped by squirrels and monkeys under the canopies of four trees. Survival as seedlings after 2 years was only 0.74 % under the tree with the highest number of dropped seeds (271) but was 20.7 % under the 3 trees with less than 100 seeds dropped. These results suggest that seed predators (probably deer) are attracted primarily to trees with large dropped crops.

Distance-dependent mortality must occur in older seedling and sapling stages to produce the spacing patterns we see on the Mo Singto plot. Evidence of such distance-dependent mortality in the sapling stage exists in other studies (Murphy et al., 2017; Stevenson, 2007; Stevenson et al., 2005; Swamy and Terborgh, 2010; Terborgh, 2020) and is possibly the result of resource competition (Lebrija-Trejos et al., 2016) from nearby large conspecifics. Such distance-dependent effects around fruiting trees may result in saplings and tree recruits up to 10 cm in dbh becoming spaced out, eventually resulting in the adult population attaining a spaced-out distribution that approaches randomness in many areas of the plot (Brockelman et al., 2017).

Despite the diversity of animals feeding on *N. melliferum* and their varied effects on dispersal, both positive and negative, some generalizations about seed dispersal are possible. Both arboreal and terrestrial mammals consume the seeds and their effects may be either positive or negative. Species interact with each other, and their effects may be contingent on each other. The fruits of

N. melliferum do not drop spontaneously from the trees, and so fruit availability for terrestrial consumers depends on the activities of arboreal frugivores. The primary mutualist seed disperser appears to be the gibbon, as suggested by several observations and lines of evidence. The seed dispersal effectiveness value across all trees was highest for gibbons, and the difference between gibbons and other dispersers was especially significant for trees with relatively large crops for which gibbons were responsible for 87% of seedlings. For small crops, *C. finlaysonii* dispersed a significant portion of seedlings (50 %) but at distances close to the parent crown where they would suffer distance-dependent effects. Unlike squirrels and monkeys, gibbons carried seeds far beyond the tree crown.

Gibbons are also highly efficient handlers of *N. melliferum* fruit. The gibbons' method of removing the fruit cover is shared with all fruit species with covers of roughly the same size (ca. 2–4 cm in diameter) and hardness (McConkey, 2000, 2009). The fruit is placed between the canines and the jaws are closed over it, so that the upper and lower incisors and the inner edges of the canines neatly cleave the rind into two halves. Gibbons, monkeys, and squirrels also differ in the way they handle the problem of removing the pulp from the seed: squirrels chew off the pulp from the seed with their incisors, monkeys suck and chew off most of the pulp and drop most seeds with part of the pulp near the seed still firmly attached, whereas gibbons simply swallow the seed with pulp attached, which is what most legitimate dispersers are found to do (Stevenson, 2011).

Gibbons are also reliable dispersers – another characteristic essential to a coevolutionary relationship (Howe and Estabrook, 1977). Individual trees are visited repeatedly as long as they are in fruit, and know the locations of all trees in fruit within their territories (Asensio et al., 2011; Suwanvecho et al., 2018), and living in long-term, permanent territories (Bartlett et al., 2016), the resident group is always available during the fruiting season. *N. melliferum* is the preferred energy source of the gibbons and is fed on almost exclusively when available (Brockelman et al., 2014; Suwanvecho et al., 2018). The staggered ripening periods of fruiting *N. melliferum* trees (Appendix B.1) also allow the gibbon group to harvest fruit from a greater number of successively ripening trees. Such a pattern has been found in gibbon-preferred fruit species at other sites (Dillis et al., 2015).

The average size of a gibbon group in Khao Yai Park is four individuals (Brockelman, 2004), which means that they have a limited capacity to consume fruits. This limitation is enforced by the strict territoriality of gibbons which, as in many songbird species in the breeding season, limits the number of frugivores that feed in fruiting trees (Bas et al., 2006; Hampe, 2008). The inability of the gibbons to track the abundance of an irregularly fruiting species such as *N. melliferum* means that in some years (as in 2004) the gibbons will have an oversupply of fruit. In 2004, gibbons consumed an estimated 19 % of the total ripe fruit crop available on the nine study trees, while squirrels consumed 56 %, monkeys consumed 9 % and 17 % was knocked off and dropped intact on the ground (Appendix B2). Deer and other ground consumers ate far more seeds than the gibbons dispersed. Despite these figures, the gibbons had the highest dispersal effectiveness. Ironically, the most effective disperser is not the most capable consumer. Terrestrial consumers such as bears and elephants may be important, however, as they have the ability to carry seeds for much longer distances, and outside the immediate forest area.

A question that bears on the coevolutionary relationship is what is the optimal crop size for a fruiting tree. If the optimal crop size is that which results in the highest percentage consumption by gibbons, then intermediate crop sizes were optimal (Appendix B). The two trees with the lowest crops (below 4000 ripe fruits per tree) had only 1.6% of fruits taken by gibbons, whereas the most productive tree (ca. 24,000 fruits) had a below-average 10 % taken by gibbons. The seven intermediate trees had 24 % of fruits taken by gibbons. In terms of numbers of fruits taken by gibbons, the most productive tree ranked 4th. Two effects seem to be operating here: a lack of interest by gibbons in trees with small crops, and their inability to take advantage of super-abundant fruit. Howe and Estabrook (1977) argued that such a pattern of declining dispersal with very high fruit availability is expected for effective and reliable specialist dispersers. Monkeys had a relatively low utilization rate of 4 %. Squirrels, on the other hand, were attracted in large numbers to the tree with the largest crop and utilized 67.5 % of ripe fruit, the highest for the nine trees. These data can only be taken as suggestive because the sample size is too small for testing a non-linear effect, and factors such as tree location and fruit quality which were not under our control. Gibbon feeding was not affected by observers because group A on the Mo Singto plot was fully habituated to human presence. Nevertheless, these results still beg the important question of why a tree should produce such a large crop if most of it is destroyed by terrestrial seed predators. We must realize that selection for crop overproduction is affected by the arboreal frugivores which are in competition with gibbons. But perhaps there is a compensating advantage in having increased chances that terrestrial dispersers will carry some seeds farther away than gibbons can travel. We may speculate that in a different forest community the results might have been different.

5. Conclusions

We have shown that gibbons pay a key role in the dispersal of *Nephelium melliferum* by having the highest dispersal effectiveness, defined as having the highest product of quantity × quality of seeds dispersed (Schupp et al., 2010). In addition to being 'effective', however, gibbons are also reliable and efficient in finding food sources, and have high preference for *N. melliferum* fruit over other species when in fruit (Asensio et al., 2011; Suwanvecho et al., 2018), which supports our first hypothesis. Our second hypothesis that gibbon dispersal compensates for negative distance-dependent survival is also supported, although the agents responsible for distance-dependent survival are not entirely clear. Deer appear to be the main source of seed and seedling mortality, but their effects are not likely to be species-specific or consistently related to distance. Our third hypothesis that gibbon consumption has limits and fails to take full advantage of very large tree crop sizes was also supported, but the limited number of trees studied render this result inconclusive, requiring further study.

Beyond our initial expectations, however, our study has yielded many other surprising findings. The first is the large number of mammal species that consume *N. melliferum* fruits or seeds, most of which are apparently opportunistic consumers. Especially surprising is the number of terrestrial mammals that take advantage of fallen fruits. Further research may show that some of these are important in distance dispersal. Of great interest are the interactions among species which determine which species get how much fruit. Such interactions, particularly among gibbons, monkeys and squirrels, result in a complex and unpredictable food web. If gibbons, as the most effective and reliable dispersers, are essential to maintaining the *N. melliferum* population, they are also essential in helping to maintain the mammal community.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02312.

References

Asensio, N., Brockelman, W.Y., Malaivijitnond, S., Reichard, U.H., 2011. Gibbon travel paths are goal oriented. Anim. Cogn. 14, 395–405. https://doi.org/10.1007/s10071-010-0374-1.

Bartlett, T.Q., 2009. The Gibbons of Khao Yai. Pearson Prentice Hall, Upper Saddle River, New Jersey.

Bartlett, T.Q., Light, L.E.O., Brockelman, W.Y., 2016. Long-term home range use use in white-handed gibbons (*Hylobates lar*) in Khao Yai National Park. Thail. Am. J. Primatol. 78, 192–203. https://doi.org/10.1002/ajp.22492.

Bas, J.M., Pons, P., Gómez, C., 2006. Exclusive frugivory and seed dispersal of *Rhamnus alaternus* in the bird breeding season. Plant Ecol. 183, 77–89.

Bascompte, J., Jordano, P., 2007. Plant-animal mutualistic networks: the architecture of biodiversity. Annu. Rev. Ecol. Evol. Syst. 38, 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818.

Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312, 431–433. https://doi.org/10.1126/science.1123412.

Brockelman, W.Y., 2004. Inheritance and selective effects of color phase in white-handed gibbons (*Hylobates lar*) in central Thailand. Mamm. Biol. 69, 73–80. https://doi.org/10.1078/1616-5047-00122.

Brockelman, W.Y., Reichard, U., Treesucon, U., Raemaekers, J.J., 1998. Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). Behav. Ecol. Sociobiol. 42, 329–339. https://doi.org/10.1007/s002650050445.

Brockelman, W.Y., 2011. Rainfall patterns and unpredictable fruit production in seasonally dry evergreen forest, and their effects on gibbons. In: McShea, W.J., Davies, S.J., Phumpakphan, N. (Eds.), The ecology and conservation of seasonaly dry forests in Asia. Smithsonian Institution Scholarly Press, Washington, DC, pp. 195–216.

Brockelman, W.Y., Nathalang, A., Greenberg, D.B., Suwanvecho, U., 2014. Evolution of small-group territoriality in gibbons. In: Yamagiwa, J., Karczmarski, L. (Eds.), Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies. Primatology Monographs. Springer, Japan, pp. 213–230. https://doi.org/10.1007/978-4-431-54523-1_11.

Brockelman, W.Y., Nathalang, A., Maxwell, J.F. (Eds.), 2017. Mo Singto Forest Dynamics Plot: Flora and Ecology. National Science and Technology Development Agency and and Department of National Parks. Wildlife and Plant Conservation, Bangkok.

Brodie, J.F., Helmy, O.E., Brockelman, W.Y., Maron, J.L., 2009. Functional differences within a guild of tropical mammalian frugivores. Ecology 90, 688–698. https://doi.org/10.1890/08-0111.1.

Bronstein, J.L., 2001. The exploitation of mutualisms. Ecol. Lett. 4, 777–787.

Bueno, R.S., Guevara, R., Ribeiro, M.C., Culot, L., Bufalo, F.S., Galetti, M., 2013. Functional redundancy and complementarities of seed dispersal by the last Neotropical megafrugivores. PLOS One 8, e56252. https://doi.org/10.1371/journal.pone.0056252.

Campos-Arceiz, A., Blake, S., 2011. Megagardeners of the forest – the role of elephants in seed dispersal. Acta Oecologica, Frugivores Seed Dispersal: Mech. Conséq. a Key Interact. Biodivers. 37, 542–553. https://doi.org/10.1016/j.actao.2011.01.014.

Carlo, T.A., Morales, J.M., 2008. Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. J. Ecol. 96, 609–618. https://doi.org/10.1111/j.1365-2745.2008.01379.x.

Carreira, D.C., Brodie, J.F., Mendes, C.P., Ferraz, K.M.P.M.B., Galetti, M., 2020. A question of size and fear: competition and predation risk perception among frugivores and predators. J. Mammal. 101, 648–657. https://doi.org/10.1093/jmammal/gyaa034.

Chamberlain, S.A., Bronstein, J.L., Rudgers, J.A., 2014. How context-dependent are species interactions? Ecol. Lett. 17, 881–890.

Dillis, C., Beaudrot, L., Feilen, K.L., Clink, D.J., Wittmer, H.U., Marshall, A.J., 2015. modeling the ecological and phenological predictors of fruit consumption by gibbons (*Hylobates albibarbis*). Biotropica 47, 85–93. https://doi.org/10.1111/btp.12176.

Fedriani, J.M., Wiegand, T., 2014. Hierarchical mechanisms of spatially contagious seed dispersal in complex seed-disperser networks. Ecology 95, 514–526. https://doi.org/10.1890/13-0718.1.

Fleming, T.H., Venable, D.L., Herrera, M., 1993. Opportunism vs. specialization: the evolution of dispersal strategies in fleshy-fruited plants. Vegetatio 107/108, 107–120.

Hai, B.T., Chen, J., McConkey, K.R., Dayananda, S.K., 2018. Gibbons (*Nomascus gabriellae*) provide key seed dispersal for the Pacific walnut (Dracontomelon dao), in Asia's lowland tropical forest. Acta Oecol. 88, 71–79. https://doi.org/10.1016/j.actao.2018.03.011.

Hammond, D.S., Brown, V.K., 1996. Disturbance, phenology and life history characteristics: factors influencing distance/density-dependen t attack on tropical seeds and seedlinbgs. In: Newberry, D.M., Prins, H.H.T., Brown, N.D. (Eds.), Dynamics of Tropical Communities. The 37th symposium of the British Ecological Society Cambridge University. Blackwell Scientific, pp. 51–78.

Hampe, A., 2008. Fruit tracking, frugivore satiation, and their consequences for seed dispersal. Oecologia 156, 137–145.

Herrera, C.M., Jordano, P., 1981. *Prunus mahaleb* and birds: the high-efficiency seed dispersal system of a temperate fruiting tree. Ecol. Monogr. 51, 203–218. https://doi.org/10.2307/2937263.

Hodgkison, R., Ayasse, M., Häberlein, C., Schulz, S., Zubaid, A., Mustapha, W.A.W., Kunz, T.H., Kalko, E.K.V., 2013. Fruit bats and bat fruits: the evolution of fruit scent in relation to the foraging behaviour of bats in the New and Old World tropics. Funct. Ecol. 27, 1075–1084. https://doi.org/10.1111/1365-2435.12101.

Howe, H.F., 2016. Making dispersal syndromes and networks useful in tropical conservation and restoration. Glob. Ecol. Conserv. 6, 152–178. https://doi.org/10.1016/j.gecco.2016.03.002.

Howe, H.F., Estabrook, G.F., 1977. On intraspecific competition for avian dispersers in tropical forests. Am. Natur. 111, 817–832.

Janson, C.H., 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. Science 219, 187–189.

Janzen, D.H., 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104, 501–528.

Jordano, P., 2000. Fruits and Frugivory. CABI Publ,, Wallingford, UK.

Jordano, P., García, C., Godoy, J.A., García-Castaño, J.L., 2007. Differential contribution of frugivores to complex seed dispersal patterns. Proc. Natl. Acad. Sci. USA 104, 3278–3282. https://doi.org/10.1073/pnas.0606793104.

José-Domínguez, J.M., Savini, T., Asensio, N., 2015. Ranging and site fidelity in northern pigtailed macaques (*Macaca leonina*) over different temporal scales. Am. J. Primatol. 77, 841–853. https://doi.org/10.1002/ajp.22409.

Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T., Noma, N., 2002. Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. Oecologia 133, 559–572. https://doi.org/10.1007/s00442-002-1073-7.

Lebrija-Trejos, E., Reich, P.B., Hernández, A., Wright, S.J., 2016. Species with greater seed mass are more tolerant of conspecific neighbors: a key driver of early survival and future abundances in a tropical forest. Ecol. Lett. 19, 1071–1080.

Levey, D.J., Benkman, C.W., 1999. Fruit–seed disperser interactions: timely insights from a long-term perspective. Trends Ecol. Evol. 14, 41–43. https://doi.org/10.1016/S0169-5347(98)01528-6.

Loayza, A.P., Knight, T., 2010. Seed dispersal by pulp consumers, not "legitimate" seed dispersers, increases *Guettarda viburnoides* population growth. Ecology 91, 2684–2695. https://doi.org/10.1890/09-0480.1.

Lynam, A.J., Round, P.D., Brockelman, W.Y., 2006. Status of Birds and Large Mammals in Thailand's Dong Payayen – Khao Yai Forest Complex. Biodiversity Research and Training Program and Wildlife Conservation Society International Programs,, Bangkok.

Marshall, A.J., Cannon, C.H., Leighton, M., 2009. Competition and niche overlap between gibbons (*Hylobates albibarbis*) and other frugivorous vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia. In: Whittaker, D., Lappan, S. (Eds.), The Gibbons. Springer, New York, New York, NY, pp. 161–188.

McConkey, K.R., 2000. Primary seed shadow generated by gibbons in the rain forests of Barito Ulu, central Borneo. Am. J. Primatol. 52, 13–29. https://doi.org/10.1002/1098-2345(200009)52:1<13::AID-AJP2>3.0.CO;2-Y.

McConkey, K.R., 2009. The seed dispersal niche of gibbons in Bornean dipterocarp forests. In: Whittaker, D., Lappan, S. (Eds.), The Gibbons. Springer New York, New York, NY, pp. 189–207.

McConkey, K.R., Brockelman, W.Y., 2011. Nonredundancy in the dispersal network of a generalist tropical forest tree. Ecology 92, 1492–1502. https://doi.org/10.1890/10-1255.1.

McConkey, K.R., Brockelman, W.Y., Saralamba, C., 2014. Mammalian frugivores with different foraging behavior can show similar seed dispersal effectiveness. Biotropica 46, 647–651. https://doi.org/10.1111/btp.12156.

McConkey, K.R., Brockelman, W.Y., Saralamba, C., Nathalang, A., 2015. Effectiveness of primate seed dispersers for an "oversized" fruit, Garcinia benthamii. Ecology 96, 2737–2747. https://doi.org/10.1890/14-1931.1.

McConkey, K.R., Nathalang, A., Brockelman, W.Y., Saralamba, C., Santon, J., Matmoon, U., Somnuk, R., Srinoppawan, K., 2018. Different megafauna vary in their seed dispersal effectiveness of the megafaunal fruit *Platymitra macrocarpa* (Annonaceae). PLOS One 13, e0198960. https://doi.org/10.1371/journal.pone.0198960.

Moermond, T.C., Denslow, J.S., 1985. Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. Ornithol. Monogr. 865–897. https://doi.org/10.2307/40168322.

Morales, J.M., Rivarola, M.D., Amico, G., Carlo, T.A., 2012. Neighborhood effects on seed dispersal by frugivores: testing theory with a mistletoe–marsupial system in Patagonia. Ecology 93, 741–748. https://doi.org/10.1890/11-0935.1.

Murphy, S.J., Wiegand, T., Comita, L.S., 2017. Distance-dependent seedling mortality and long-term spacing dynamics in a neotropical forest community. Ecol. Lett. 20, 1469–1478.

Naoe, S., Tayasu, I., Sakai, Y., Masaki, T., Kobayashi, K., Nakajima, A., Sato, Y., Yamazaki, K., Kiyokawa, H., Koike, S., 2016. Mountain-climbing bears protect cherry species from global warming through vertical seed dispersal. Curr. Biol. 26, R315–R316. https://doi.org/10.1016/j.cub.2016.03.002.

Palmer, T.M., Pringle, E.G., Stier, A., Holt, R.D., 2015. Mutualisms in a community context. In: Bronstein, J.L. (Ed.), Mutualism. Oxford University Press, Oxford, pp. 158–180.

Peña-Egaña, M., Loayza, A.P., Squeo, F.A., 2018. Are pulp consumers effective seed dispersers? Tests with a large-seeded tropical relict tree. Biotropica 50, 898–907. https://doi.org/10.1111/btp.12604.

Perea, R., Delibes, M., Polko, M., Suarez-Estaban, A., Fedriani, J.M., 2013. Context-dependent fruit-frugivore interactions: partner identities and spatio-temporal variations. Oikos 122, 943–951.

R Core Team. (2021). An introduction to R. 〈https://cran.r-project.org/doc/manuals/r-release/R-intro.html〉. Downloaded on 28–04-2021.

Rother, D.C., Pizo, M.A., Jordano, P., 2016. Variation in seed dispersal effectiveness: the redundancy of consequences in diversified tropical frugivore assemblages. Oikos 125, 336–342. https://doi.org/10.1111/oik.02629.

Rothman, J.M., Raubenheimer, D., Chapman, C.A., 2011. Nutritional geometry: gorillas prioritize non-protein energy while consuming surplus protein. Biol. Lett. 7, 847–849. https://doi.org/10.1098/rsbl.2011.0321.

Schupp, E.W., 1993. Quantity, quality and effectiveness of seed dispersal by animals. Vegetatio 107/108, 15–27.

Schupp, E.W., Jordano, P., Gómez, J.M., 2010. Seed dispersal effectiveness revisited: a conceptual review. N. Phytol. 188, 333–353. https://doi.org/10.1111/j.1469-8137.2010.03402.x.

Stevenson, P.R., 2007. A test of the escape and colonization hypotheses for zoochorous tree species in a Western Amazonian forest. Plant Ecol. 190 (2), 245–258.

Stevenson, P.R., 2011. Pulp-seed attachment is a dominant variable explaining legitimate seed dispersal: a case study on woolly monkeys. Oecologia 166, 693–701.

Stevenson, P.R., Link, A., Gonzalez-Caro, S., Torres-Jimenez, M.F., 2015. Frugivory in canopy plants in a western Amazonian forest: dispersal systems, phylogenetic ensembles and keystone plants. PLos One 10, e0140751. https://doi.org/10.1371/journal.pone.0140751. In this issue.

Stevenson, P.R., Link, A., Ramírez, B.H., 2005. Frugivory and seed fate in *Bursera inversa* (Burseraceae) at Tinigua Park, Colombia. Biotropica 37, 431–438. https://doi.org/10.1111/j.1744-7429.2005.00057.x.

Stoner, K.E., Riba-Hernández, P., Vulinec, K., Lambert, J.E., 2007. The role of mammals in creating and modifying seed shadows in tropical forests and some possible consequences of their elimination. Biotropica 39, 316–327.

Sushma, H.S., Singh, M., 2008. Hunting of Indian giant squirrel (*Ratufa indica*) by the lion-tailed macaque (*Macaca silenus*) in the Western Ghats, India. Curr. Sci. 95, 1535–1536.

Suwanvecho, U., Brockelman, W.Y., Nathalang, A., Santon, J., Matmoon, U., Somnuk, R., Mahannop, N., 2018. High interannual variation in the diet of a tropical forest frugivore (*Hylobates lar*). Biotropica 50, 346–356. https://doi.org/10.1111/btp.12525.

Swamy, V., Terborgh, J.W., 2010. Distance-responsive natural enemies strongly influence seedling establishment patterns of multiple species in an Amazonian rain forest. J. Ecol. 98 (5), 1096–1107.

Tan, K.H., Zubaid, A., Kebangsaan, M.U., Kunz, T.H., 2000. Fruit dispersal by the lesser dog-faced fruit bat, Cynopterus brachyotis (Muller) (Chiroptera: Pteropodidae). Malay. Nat. J. Malays.

Terborgh, J., 2020. At 50, Janzen–Connell has come of age. BioScience. https://doi.org/10.1093/biosci/biaa110.

Terborgh, J., Losos, E., Riley, M.P., Bolaños Riley, M., 1993. Predation by vertebrates and invertebrates on the seeds of five canopy tree species of an Amazonian forest. Vegetatio 107, 375–386.

Thompson, J.N., 1988. Variation in Interspecific Interactions. Ann. Rev. Ecol. Syst. 19, 65–88.

Thompson, J.N., 2005. The geographic mosaic of coevolution. University of Chicago Press, Chicago.

Vimuktayon, P., 2001. The ecology of seed dispersal in wild rambutan (*Nephelium melliferum*) by white-handed gibbons (*Hylobates lar*) and other frugivores in Khao Yai National Park, Thailand (M.Sc. dissertation). Mahidol University, Bangkok.

Wenny, D.G., 2000. Seed dispersal, seed predation, and seedling recruitment of a Neotropical montane tree. Ecol. Monogr. 70, 331–351.

Zwolak, R., Sih, A., 2020. Animal personalities and seed dispersal: a conceptual review. Funct. Ecol. 34, 1294–1310. https://doi.org/10.1111/1365-2435.13583.