

Secondary removal of seeds dispersed by gibbons (*Hylobates lar*) in a tropical dry forest in Thailand

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Abstract. Many animal-dispersed seeds are subject to post-dispersal removal by vertebrate and invertebrate organisms resulting in further dispersal or predation. A field experiment was carried out to study seed removal of six gibbon-dispersed seed species in a tropical dry forest in central Thailand during the wet season of 2016 and early dry season of 2017. We collected seeds from the defecations of four groups of white-handed gibbon (*Hylobates lar*), of which two groups lived in an evergreen forest habitat and two groups in a mosaic habitat composed of mixed-deciduous forest and dry-dipterocarp forest. We used camera traps to monitor seed removal activities of the rodents. Rodents had the most impact on the seeds dispersed by the gibbons. *Maxomys surifer*, the red-spiny rat was the most abundant ground-dwelling rodent species, and accounted for the greatest proportion of seed removal events, followed by *Leopoldamys sabanus*, the long-tailed giant rat, which was less abundant. The study also found that invertebrates, in particular ants, were important in post-dispersal seed removal. Seed removal by both rodents and invertebrates as well as by *M. surifer* alone did not differ significantly between the two habitat types. Further and longer-termed study is suggested to understand the competitive relationship between the rodents and invertebrates as well as the impacts habitat type and seasonality on seed fates.

Key words. Post-dispersal seed removal, rodents, tropical dry forest, habitat type

INTRODUCTION

In Southeast Asia, gibbons (Hylobatidae) are seed dispersers for hundreds of plant species (McConkey, 2000) due to their highly frugivorous diet (Kinnaird & O'Brien, 2005) which includes fruit species potentially important as food resources for numerous other frugivores in the region (McConkey, 2009). Gibbons are known to utilise often patchily-distributed fruit resources via daily ranging (Asensio et al., 2011; Brockelman et al., 2014). Most seeds found in their faeces are intact (McConkey, 2009), suggesting that seeds are swallowed whole rather than chewed which would otherwise result in seed mortality (Lambert & Garber, 1998). The efficiency of gibbon seed dispersal can be assessed by estimating seeds that survive foraging by post-dispersal seed predators (McConkey & Brockelman, 2011). However, what happens to seeds after they are dispersed by the gibbons is largely unknown.

Removal of primate-dispersed seeds has important implications to seed survival, plant regeneration dynamics and forest regeneration in the tropical Asian forests (Gleaves, 2013). Post-dispersal seed removal may imply seed predation or secondary dispersal, with rodents and ants being two

frequent animal groups reported to play an important role (Blackham & Corlett, 2015) for seeds dispersed by primary dispersers like the gibbons (McConkey, 2005). And murid rodents (predominantly species from the subfamily Murinae, Old World rats and mice) occupying mid-to-lower forest canopies have been found to be especially efficient in removing large quantities of seeds dispersed (DeMattia et al., 2004; Blackham & Corlett, 2015; Horst & Venable, 2017).

Rodents can locate seed deposits using odors (Wallace et al., 2002), and process seeds with penetrating incisors (Hulme & Benkman, 2002), whereas surplus seeds may be further carried away and buried for later consumption. Secondary dispersal of seeds by scatter-hoarding rodent species (Forget & Milleron, 1991; Jansen & Forget, 2001), including those utilising multiple caches of dispersed seeds, has also been documented (Jansen et al., 2012). The efficiency of rodents indicated by the quantities of seeds removed (Janzen, 1971), with seed size potentially affecting seed removal rates (Gleaves, 2013) can lead to significant consequences in plant establishment of seed-limited plant species (Turnbull et al., 2000; Vander Wall et al., 2005). Studies of rodent seed predation and secondary dispersal frequently focus on their impact on seed survival (Stephens et al., 2012; Leiva & Díaz-Maqueda, 2016) and plant population dynamics (Fedriani & Manzan, 2005; Alcántara et al., 2000; Bricker & Maron, 2012). However, rodent density is thought to respond to changes in food availability (Brown & Munger, 1985), predators (Huitu et al., 2004), interspecific competition (Eccard & Ylönen, 2003) and fire (Walker & Rabinowitz, 1992). Differences in vegetation characteristics can also affect rodent distributions and local abundance, e.g. primary

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versus disturbed habitats (Mittelbach & Gross, 1984), habitats with or without fragmentation (Santos & Telleria, 1997), and distance from the forest edge (Holl & Lulow, 1997).

Tropical dry forest often contains a variety of vegetation types occurring along a moisture gradient (Chaturvedi et al., 2012), and also represents a special context for the study of habitat relationships with ecological processes as more than one habitat type can co-occur within short geographic distances (Murphy & Lugo, 1986). During the fruiting season in dry forest, consumption of fruits and transportation of their seeds plays an important role in the dispersal of many species (Griz & Machado, 2001). Endozoochory is seed-dispersal via animal consumption and defecation (Carlo et al., 2007), but the seeds dispersed are yet vulnerable to predators (both vertebrates and invertebrates) actively seeking food on the ground (Janzen, 1971). Despite the wide distribution of rodents which occupy almost all terrestrial ecosystems (Hafner & Hafner, 1988), their role in the post-dispersal of seeds in tropical dry forest and how different habitat types within these dry forests affect this role is poorly known.

In the tropical dry forest of central Thailand, gibbons were found to inhabit both evergreen habitat and a mosaic habitat (a combination of mixed-deciduous and dry-dipterocarp forest types) (Light, 2016). Nine rodent species were found in the two habitat types (Walker & Rabinowitz, 1992). While rodents are cited as seed predators (Galetti et al., 2015; Pearson et al., 2014) and secondary seed dispersers (Corlett, 2017), the role of the rodents in the dry tropical forest in Southeast Asia has also rarely been studied.

The aim of this work is to investigate seed removal by rodents on six seed species dispersed by gibbons in different habitat types. Because of the proven efficiency of rodent seed-removal on primate-dispersed seeds in other tropical ecosystems (Corlett, 2016), we hypothesised that rodents were the most frequent group of animals to remove mid-to-large-sized (diameters >1 cm) seeds dispersed by the gibbons and that the intensity of seed removal of gibbon-dispersed seeds was different between the mosaic and evergreen habitat types. We predicted that rodents would be responsible for most of the seed removal from the site of deposition and that the habitat with the higher density of rodents would have correspondingly higher seed removal intensity than the habitat type with lower rodent density.

MATERIAL & METHODS

Study site. The study was carried out from June to December 2016, and February to March 2017 in a tropical dry forest near the Khao Nang Rum Wildlife Research Station (KNR) (15°25'–15°31'N, 99°15'–99°20'E), Huai Kha Khaeng Wildlife Sanctuary in central Thailand. Huai Kha Khaeng Sanctuary (2,575 km²) is one of the 17 nature reserves of the Western Forest Complex (Bunyavejchewin et al., 2004). The forest near KNR is primary with the only disturbance from annual fires (Baker & Bunyavejchewin, 2009) which are set by park staff as part of the management as well as those set by local people likely for purposes of hunting and

mushroom collection (Himmapan & Kaitpraneet, 2007). The fires however may drastically reduce food sources critical to the survival of small mammals (Walker & Rabinowitz, 1992).

The rainy season of 2016 was from late May to October, followed by the dry season, which began in November. Cumulative precipitation from June to October was 1,980 mm, compared to 200 mm from November 2016 to March 2017. Sporadic rainstorms were recorded in January (33 mm) and March (94 mm) 2017. February and March in 2017 were also the fire season with part of the study area burnt. Average temperature from June 2016 to March 2017 was 23.4°C. Daily temperature and precipitation were measured by a weather station situated in the administrative area of KNR Station.

The forest near KNR is composed of three different types: evergreen forest, mixed-deciduous forest and dry-dipterocarp forest (Walker & Rabinowitz, 1992). The evergreen forest is distributed mainly at the foothills of Khao Khiao (highest peak in the area) where a permanent river runs through. It has a relatively reduced understory layer (Walker & Rabinowitz, 1992) which may offer little shelter for small mammals. Relatively aseasonal, the evergreen forest had the highest species diversity (Baker et al., 2005) and fruit productivity, compared to the two other forest types (Light, 2016). The mixed deciduous forest is the dominant forest type in the study area (Fig. 1). The dense understory of the mixed-deciduous forest can serve as shelter for small mammals. The dry-dipterocarp forest is found in places with little or no surface water, and is species-poor (Light, 2016). It is dominated by tree species mainly from the genera *Shorea* and *Dipterocarpus* (Dipterocarpaceae) (Bunyavejchewin et al., 2011). Many plant species in the dry-dipterocarp forest have acquired fire-resistance traits, such as a thick bark (Wolseley & Aguirre-Hudson, 1997). The poorly-developed understory of the dry-dipterocarp forest also probably offers little shelter for small mammal species.

Fifteen white-handed gibbon (*Hylobates lar*) groups were observed in the forest near KNR, with five groups from the evergreen habitat and 10 groups from a mosaic of mixed-deciduous and dry-dipterocarp forest (referred to as the mosaic habitat) (Light, 2016). Among them, four groups (A, B, D, and L) were habituated to people. A total of 16 individuals were counted in the four habituated groups, each group containing 4–5 gibbons. According to Light (2016), Group A and Group B are neighboring groups inhabiting the (mostly) evergreen habitat (55.5% evergreen forest, 42.8% mixed-deciduous forest, and 1.7 % dry-dipterocarp forest), and group D and group L are neighboring groups in the mosaic habitat (58% mixed-deciduous forest, 39.8% dry-dipterocarp forest, and 2.3% evergreen forest).

Rodent community and live-trapping. Nine rodent species (six murid species: *Maxomys surifer*, *Leopoldamys sabanus*, *Rattus rattus*, *Niviventer bukit*, *Berylmys berdmorei*, and *Mus cervicolor*; and three non-murid species: *Menetes berdmorei*, *Hystrix brachyura*, and *Atherurus macrourus*) were found near KNR (Walker & Rabinowitz, 1992; Dai,

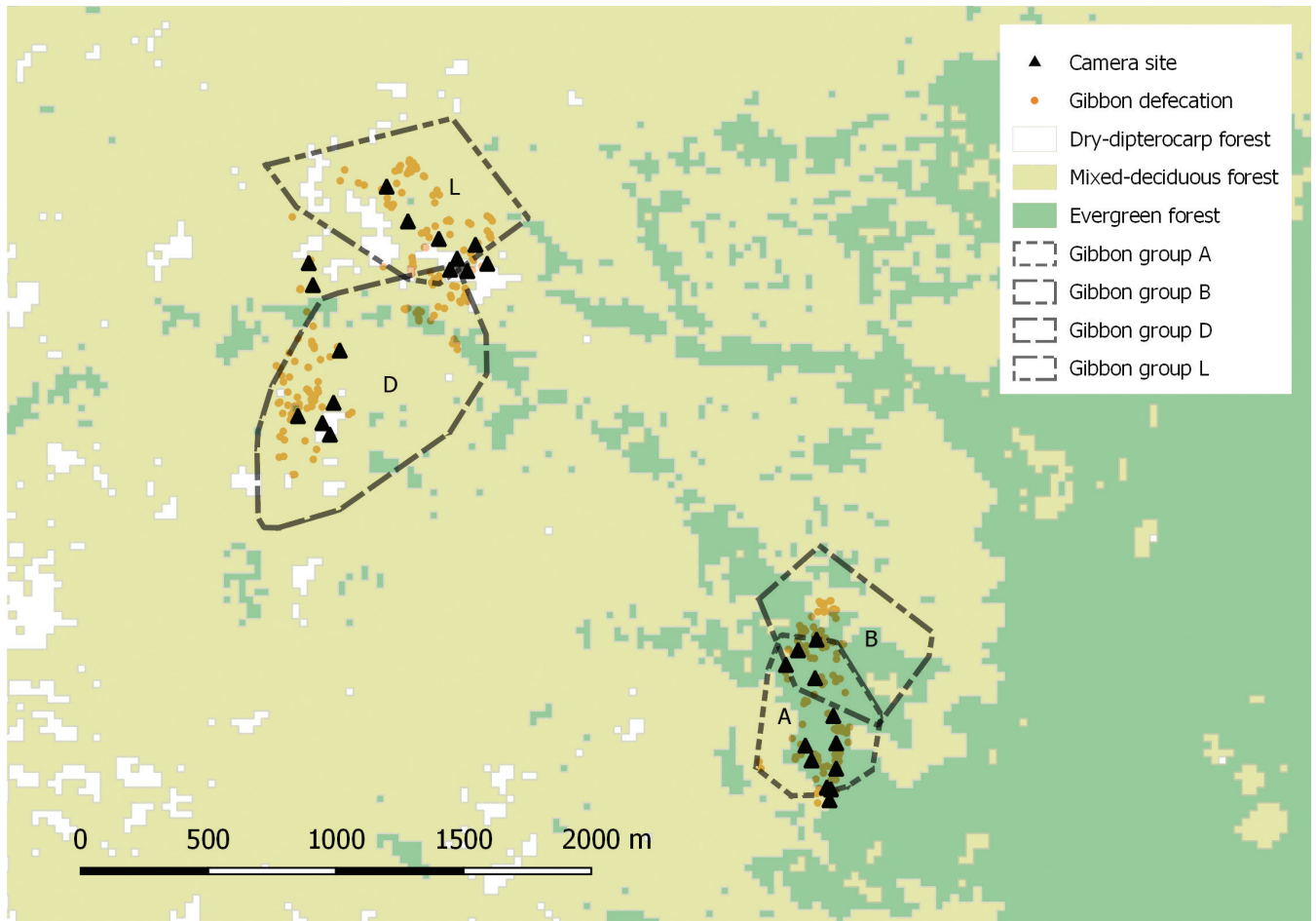


Fig. 1. Distribution of experimental sites where seeds were dispersed by 4 groups of white-handed gibbons (*Hylobates lar*). Home range maps of the gibbons are based on Light (2016) and Phiphatsuwannachai et al. (2018), plus newly-discovered areas (extended home ranges) by the author. Fruiting trees and gibbon defecation locations were recorded in a GPS. Each site when active contained a camera trap and a paired control/treatment.

personal observation). Among the three most abundant murid rodents, *M. surifer* (red-spiny rat) and *L. sabanus* (long-tailed giant rat) are mainly found in primary and secondary forests (Pimsai et al., 2014), and *R. rattus* (black rat) are typically associated with disturbed landscapes (e.g. agricultural pasture, secondary forests etc., viz. Stephenson, 1995). All rodent species except *M. berdmorei* are nocturnal, with *H. brachyura* being occasionally diurnal (Dai, personal observation).

To investigate rodent densities and differences in the two habitats (mosaic vs. evergreen), four short small mammal trapping sessions were carried out in July 2016, December 2016, February 2017, and March 2017. Each session lasted for seven days (or six nights) avoiding full-moon periods. A total of 60 traps were used including 58 Sherman traps (14 S-sized: $8 \times 9 \times 24$ cm, 44 L-sized: $10 \times 12 \times 38$ cm) and two locally-made traps ($35 \times 18 \times 18$ cm). During the March session, due to elephant (*Elephas maximus*) damage only 52 traps were used. The traps were divided into two trapping grids, each (150×125 m) containing 30 traps (26 traps for March session). In one grid, each trap was 25 m from the neighboring traps. Each grid was in one habitat, with the evergreen grid within the evergreen habitat of gibbon group A's home range and the mosaic grid within the mosaic habitat gibbon group D's home range. Distance

between the two trapping grids was approximately 2.4 km.

Traps were baited with bananas, sweet potatoes, and sweet corn. A metal hook was used for the bait to secure it above the trap floor to reduce the impact of ants. Traps were baited between 1500 and 1730 hours every day and were checked in the following morning at 0800–1100 hours. Once a rodent was found in the trap, it was immediately identified to species, sexed, measured (body length: from nose to tail base, and tail length: from anus to tail tip), marked with a uniquely numbered metal ear tag, and then released where it had been captured. Identification of rodent species followed Pimsai et al. (2014). Rodent density was calculated using the secr package (Efford, 2017) within program R (R Development Core Team, 2017a) with R Studio (R Development Core Team, 2017b).

Seed removal experiment. Each gibbon group (A, B, D, and L) was followed for 2–3 consecutive days in June 2016, September to November 2016, and March 2017 by multiple observers who collected fecal samples when defecation occurred. Geographic locations of all observed fruiting plants (including trees and lianas) and defecation points (Fig. 1) were recorded using a handheld GPS device (Garmin eTrex T300, Garmin Ltd.).

Faeces were then briefly rinsed with water to separate the seeds from the rest of the fecal matter. Seeds were counted, air-dried and stored at room temperature until used for the experiment. And here we report the results of experiments with six commonest seed species (mean length = 1.73 cm, ranging from 1.13 to 3.59 cm; Table 2). A small amount of seeds from each of the six species (except *Walsura robusta*, which began to germinate soon after collection) were preserved for identification. Species identification for *Irvingia malayana*, *Microcos tomentosa*, and *Uvaria rufa* followed Gardner et al. (2000) and Li & Gilbert (2011), and species identification for other seed species were through personal communications with W. Brockelman (for *Uvaria lucida*), with R. Buasalee (for *W. robusta*) and with T. Caughlin (for *Milusa horsfieldii*). Supplemental seeds for *I. malayana* were collected due to the insufficient amount found in the gibbon faeces. Supplemental seeds were obtained from fresh fruits by manually removing fruit pulp, and from deer-regurgitated seed piles located often near the fruiting trees. Only intact seeds with no microbial infestation or insect holes were collected and used for the experiment.

The experiment used a paired control (rodent-free) and treatment (rodent-excluded) to test the impact of rodents on seeds assigned to the experiment. Camera traps were used to monitor seeds and their removal by rodents and other vertebrate predators/dispersers. In total 27 sites (12 in the evergreen forest, 9 in the mixed-deciduous forest, and 6 in the dry-dipterocarp forest) were selected within the homerange of the four gibbon groups (Fig. 1). Thirteen sites were used for experiment in the early wet season (June–September 2016), and fourteen sites were used in the late wet season and early dry season (September–December 2016). Each site was at least 50 m from one another except one site in the evergreen forest, which was only 20 m from the nearest site. Selected sites avoided places near the fruiting plants to reduce the impact of seed rain. Slopes over 20° were also avoided to prevent seeds moving due to gravity.

The cameras (HCO-Scoutguard SG565F-white flash) were set 0.6 m high, and each was 2.5 m away from the control and treatment. Cameras were set to operate for 24 hours per day without delay between photos. In the rodent-excluded treatment, a cage (12 × 12 × 6 cm) made of metal mesh wire (mesh size: 1 × 1 cm) was used to protect the seeds from being removed by rodents and animals larger than rodents. The cage was fixed with wooden sticks at four corners with the cage walls buried into the soil at a depth of 3 cm. Seeds were simply put on the ground in the control. Distance between the control and treatment was 30 cm. For experiments running during the rainy period (June to September 2016), a wooden frame was used to encircle the control and the treatment to reduce the impact of rain-wash.

Seed addition and quantifying seed loss using camera images. Collected seeds were added in equal numbers to the controls and the treatments. Each observation (control/treatment) contained a single seed species. Multiple seed species used in one site were marked as “mixed” in order to distinguish from single-species sites. Number of seeds

per observation varied between 1–30 (Table 2) depending on the availability. For *I. malayana*, *M. horsfieldii*, *M. tomentosa*, *U. lucida*, and *W. robusta* seeds were lined up in rows each containing up to 10 seeds, with 2–3cm between neighboring seeds. Due to their small size and resemblance to the background color of the forest floor, *U. rufa* was used at up to 30 seeds per observation and seeds were clumped to optimise visibility, and seed loss was measured by estimation from the photographs.

Seeds were then left for over seven days before checking. Sites were examined 1–3 times per month between June to December, during which process numbers of seeds in each species were counted, and their status (germinated, infected by microbes, showing signs of insect attack [exit holes], etc.) noted. A total of 108 seeds affected by microbes and insects were removed from the experiments. Final checks took place on 24 February 2017 for sites in the mosaic habitat, and on 9 March 2017 for sites in the evergreen habitat. And the time periods (counted in days) between the date when the seeds were assigned and the date of final check were treated as a variable (“day”, see Data analysis section below).

With the camera response time set to 0 seconds, one image with one or more animals in it was considered a single visit, and 2 visits (by the same species) if the visits were at least 30 min from one another (Suzuki et al., 2007). A general definition of seed removal (Blackham & Corlett, 2015) was used in which a seed was displaced (which may involve seed predation or secondary dispersal) from the site, or showed signs of insect attack or infection by microbes. We defined seed removal by a rodent if one of the following occurred: (1) a rodent was observed touching (usually with its nose or its mouth) seeds on the ground, (2) a rodent was observed carrying seed(s) in its mouth, or (3) rodent-only (without touching/carrying seeds) images coupled with reduction of seed(s). The same assumptions also applied to other mammals. Losses of seeds in the treatment were noted as removal by invertebrates except where trap camera images showed intrusions into the cages by rodents or other mammals.

Based on the images, identification of the three most commonly photographed murid rodents was assessed using the following criteria: 1) body length more than 20 cm and tail length being ~ 140% of body length was classified as *L. sabanus*; 2) body length of similar length to tail length, both of ~ 16 cm for *M. surifer*; 3) body length similar to tail length, both being less than 16 cm for the *Rattus* species (Pimsai et al., 2014). The *Rattus* species was further distinguished by a light/dark gray coat whereas those of *M. surifer* and *L. sabanus* were often orange-to-red.

Data analysis. Binomial regression was used to access the impact of: physical factors (elevation and rainfall), habitat type (mosaic vs. evergreen), animal type (rodents vs. invertebrates) and experimental modification (seed species, mixture versus single seed species, day and cage treatment) on seed removal intensity, defined as the proportion of seeds taken by certain animals. Rainfall can suppress rodent

Table 1. Rodent density estimates for 4 trapping sessions, July and December 2016, February and March 2017. Density was estimated for two habitat types: mosaic and evergreen, for all species combined (*M. surifer*, *L. sabanus*, *M. cervicolor*, and an unknown *Rattus* species) and for the dominant species, *M. surifer* only. D = density, SE = standard error, LCI = lower limit of 95% confidence interval, and UCI = upper limit of the 95% confidence interval.

	July				December				February				March			
	D	SE	LCI	UCI	D	SE	LCI	UCI	D	SE	LCI	UCI	D	SE	LCI	UCI
Evergreen habitat																
All spp.	1.61	0.76	0.67	3.86	3.22	1.12	1.67	6.23	5.48	1.54	3.20	9.39	4.51	1.36	2.53	8.05
<i>M. surifer</i>	1.56	0.73	0.65	3.73	3.12	1.08	1.61	6.03	5.30	1.49	3.08	9.09	4.05	1.26	2.23	7.36
Mosaic habitat																
All spp.	3.22	1.12	1.67	6.23	4.51	1.36	2.53	8.05	11.60	2.53	7.61	17.70	7.73	1.92	4.79	12.48
<i>M. surifer</i>	3.12	1.08	1.61	6.03	3.74	1.20	2.02	6.92	10.59	2.36	6.88	16.31	6.85	1.76	4.18	11.24

activities (Vickery & Bider, 1981); values of rainfall were averaged over 7-day periods starting on the day when seeds were set in each experiment. We used the number of seeds lost during each observation relative to the total seeds lost at the final check as an index for seed removal intensity. A global model, which included all the variables was constructed to test for overdispersion. Model averaging was performed based on model uncertainty ($\Delta AICc < 2$) using the “MuMIn” package (Barton, 2018), and a subset of models accumulating to 95% of the AICc weights were reported.

We then used observations of *M. surifer* alone, by far the most frequent rodent (see Results section below) to further examine the impact of habitat on seed removal by this dominant predator/secondary disperser. Since number of observations ($N = 49$) for *M. surifer* was limited, the second regression analysis contained only three variables (“day”, “elevation” and “habitat”); we tested the individual effects of each of these variables in three additional models, and compared their AIC values.

RESULTS

Rodent community and density. Five rodent species: *M. surifer*, *L. sabanus*, *H. brachyura*, *A. macrourus*, and *M. berdmorei* were identified from camera trap images while rodent trapping caught four murid rodent species (*M. surifer*, *L. sabanus*, *M. cervicolor*, and *Rattus* species) and no non-murid rodents were caught. In total 118 individuals were caught in the four trapping sessions. *Maxomys surifer* (106 individuals) counted for the majority of the captures, followed by the *Rattus* species (6 individuals), *L. sabanus* (5 individuals), and *M. cervicolor* (1 individual). Murid rodent density did not differ significantly between the two habitat types, however, density estimates tended to be higher (for all species) in the mosaic habitat compared to the evergreen habitat in each of the four months trapping was conducted (Table 1).

Seed removal experiment. In total, 134 observations (67 pairs of controls and treatments; 48 observations in the evergreen habitat and 86 observations in the mosaic habitat) were made, among which 119 with identified animals: rodents (62 observations), invertebrates (57 observations), and in 15 observations no animals were observed to have impact on seed removal (i.e., animal appeared in the images, but with no reduction in seed number). Based on the camera images, seed removal by the rodents took place between 1730–0400 hours. Five (*M. surifer*, *L. sabanus*, *Rattus* species, *H. brachyura*, and *M. berdmorei*) were observed directly or potentially affecting (e.g., *M. berdmorei* was observed in one case biting the protective cage with 4 seeds of *I. malayana* in it, but was unable to get access to) the seeds. Among the 62 observations of rodent seed removal, *M. surifer* was the most frequent animal species (49 observations [79.0%]), followed by *L. sabanus* (11 observations [17.7%]), *H. brachyura* (one observation [1.6%]), and the unknown *Rattus* species (1.6%). Rodent seed removal rate (removed/assigned seed numbers) was 97% compared to 77% for invertebrates (Table 2). The time between when the seeds were set in the experiment and when they were removed by rodents was relatively short (mean = 2.65 days).

We also found that invertebrates, especially ants were important, removing an estimated 699 seeds (compared to 626 seeds by rodents). Ants of genus *Pheidole* were seen both removing and consuming seeds of *Uvaria rufa*. Infestations by microbes of unidentified species were observed in all six seed species used in the field experiments. Most seeds removed by invertebrates were from the cage treatment ($N = 543$ seeds) compared to the open controls ($N = 156$ seeds) whereas most seeds removed by rodents were from the open controls ($N = 562$ seeds) compared to the cage treatment ($N = 64$ seeds). The significant difference ($\chi^2 = 605.38$, $k = 1$, $p < 0.001$) between seed removal in the control and treatment by the two animal types suggested that under the natural conditions (i.e., without the protective cage) more seeds would be removed by the rodents (Table 2).

Table 2. Seed removal experiment using 6 species of seeds with length > 1 cm collected from gibbon faeces and from supplemental sources. *Walsura robusta* was found only in the mosaic habitat in the faeces of the gibbons. Seeds from both the controls and treatments were included, and seeds removed were assessed based on camera trap images (for rodent removal) and direct inspection of seeds. The removal rate is the total number of seeds removed versus the number assigned for all trials combined for each seed species per habitat.

Scientific name (family)	Plant type	Seed size: length × width (cm)	Mosaic habitat					Evergreen habitat				
			Number of trials	Number of seeds used in treatment	Total seeds assigned (removal rate)	Removed by rodents	Removed by invertebrates	Number of trials of seeds used in treatment	Total seeds assigned (removal rate)	Seed removed by rodents	Removed by invertebrates	
1) <i>Irvingia malayana</i> (Irvingiaceae)	Tree	3.59 × 2.45	18	1/2/3/6	38 (84%)	32	0	14	4/5	58 (59%)	34	0
2) <i>Microcos tomentosa</i> (Malvaceae)	Tree	1.13 × 0.90	8	5	20 (85%)	17	0	4	5	20 (30%)	5	1
3) <i>Mitusa horsfieldii</i> (Annoaceae)	Tree	1.46 × 0.90	10	10/20	140 (55%)	40	37	10	10/25	160 (37%)	0	59
4) <i>Uvaria lucida</i> (Annoaceae)	Shrub	1.93 × 0.83	10	5/10	70 (99%)	40	29	14	5	70 (97%)	35	33
5) <i>Uvaria rufa</i> (Annoaceae)	Shrub	1.13 × 0.60	30	10/20/ 30	720 (100%)	250	469	6	30	180 (100%)	120	60
6) <i>Walsura robusta</i> (Meliaceae)	Tree	1.14 × 0.96	10	3/10/20	103 (62%)	53	11	NA	NA	NA	NA	NA

Table 3. (1) Model selection of 36 sub-models with accumulated 95% model weights in a binomial regression analysis of seed removal. Factors in the models were: elevation (465–722 m), habitat (mosaic vs. evergreen), animal (rodents vs. invertebrates), day (number of days starting from when the seeds were assigned until the end of a given experiment, ranging from 7–188), seed (*I. malayia*, *M. tomentosa*, *M. horsfieldii*, *U. lucida*, *U. rufa*, and *W. robusta*), mix (the effects of more than 1 seed species in the same experiment), rainfall (0–35.3 mm) and treatment (open control vs. cage treatment). df is degree of freedom and wi is model weight. (2) Models assessing factors affecting the impact of *Maxomys surifer*, the dominant rodent species, on seed removal (only three variables were tested: day, elevation, and habitat).

(1) of rodents and invertebrates on seed removal		df	AICc	ΔAICc	wi
1	elevation + habitat + animal + seed + treatment	11	272.9	0	0.17
2	day + elevation + habitat + animal + seed + treatment	12	274.67	1.77	0.07
3	elevation + habitat + animal + rain + seed + treatment	12	274.74	1.83	0.07
4	elevation + habitat + animal + seed	10	275.11	2.21	0.06
5	day + elevation + habitat + animal + rain + seed + treatment	13	275.2	2.29	0.05
6	elevation + habitat + mix + animal + seed + treatment	12	275.31	2.41	0.05
7	animal + rain + seed + treatment	10	275.46	2.55	0.05
8	animal + seed + treatment	9	275.84	2.94	0.04
9	day + animal + rain + seed + treatment	11	276.78	3.88	0.02
10	day + habitat + animal + rain + seed + treatment	12	276.97	4.06	0.02
11	day + elevation + habitat + animal + seed	11	277.03	4.13	0.02
12	elevation + habitat + animal + rain + seed	11	277.11	4.21	0.02
13	day + elevation + habitat + mix + animal + seed + treatment	13	277.12	4.22	0.02
14	habitat + animal + rain + seed + treatment	11	277.13	4.23	0.02
15	elevation + habitat + mix + animal + rain + seed + treatment	13	277.18	4.28	0.02
16	elevation + habitat + mix + animal + seed	11	277.19	4.29	0.02
17	elevation + animal + seed + treatment	10	277.24	4.33	0.02
18	day + elevation + habitat + mix + animal + rain + seed + treatment	14	277.65	4.75	0.02
19	mix + animal + rain + seed + treatment	11	277.81	4.91	0.01
20	elevation + animal + rain + seed + treatment	11	277.83	4.93	0.01
21	mix + animal + seed + treatment	10	277.97	5.07	0.01
22	day + animal + seed + treatment	10	278.02	5.12	0.01
23	habitat + animal + seed + treatment	10	278.15	5.25	0.01
24	day + elevation + habitat + animal + rain + seed	12	278.21	5.31	0.01
25	animal + rain + seed	9	278.46	5.55	0.01
26	day + elevation + animal + rain + seed + treatment	12	278.85	5.94	0.01
27	day + mix + predator + rain + seed + treatment	12	279.16	6.26	0.01
28	elevation + habitat + mix + animal + rain + seed	12	279.21	6.3	0.01
29	day + elevation + habitat + mix + animal + seed	12	279.26	6.35	0.01
30	habitat + mix + animal + rain + seed + treatment	12	279.38	6.48	0.01
31	day + habitat + mix + animal + rain + seed + treatment	13	279.42	6.51	0.01
32	animal + seed	8	279.47	6.57	0.01
33	day + elevation + animal + seed + treatment	11	279.54	6.64	0.01
34	elevation + mix + animal + seed + treatment	11	279.6	6.69	0.01
35	elevation + animal + seed	9	279.82	6.92	0.01
36	day + animal + rain + seed	10	279.87	6.96	0.01

(2) of <i>M. surifer</i> on seed removal					
1	day	2	71.73	0.00	0.99
2	elevation	2	81.27	9.54	0.01
3	habitat	2	83.87	12.14	0.00

For the global model with rodent and invertebrate removals pooled, overdispersion (residual deviance/df = 1.39) was small and therefore was ignored. We generated a subset of 36 models accounting for 95% of model weights (Table 3). The most parsimonious model accounted for 17% of the AICc weight. Model-averaged results (Table 4) suggested that animal type (rodents) and seed species (primarily *U. rufa* and *U. lucida*) were the most supported factors underlying seed

removal intensity. Visualised model-averaging results (Fig. 2) also indicated that the variable ‘rodents’ had strong support. The models also indicated that the cage treatment tended to reduce seed removal rates, although the 95% confidence interval of the estimated regression coefficient overlapped zero (Table 4, Fig. 2). The models further suggested that seed removal rates were not different between the two habitat types (Table 4, Fig. 2).

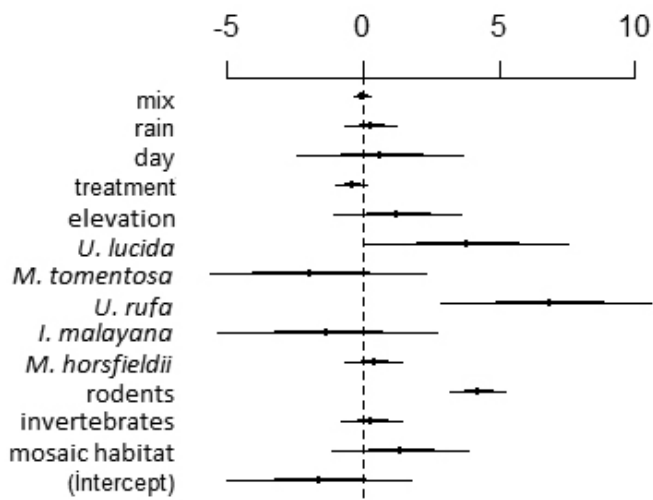


Fig 2. Estimates of beta-coefficients from binomial regressions with parameter estimates derived from model averaging with 95% confidence intervals. A variable is considered significant if the confidence interval does not overlap zero.

By testing the impact of *M. surifer* alone, we found that the model with “day” (number of days seeds were at risk to predation during the field experiment) had substantially more support than elevation or habitat (Table 3), with a strong negative effect [coefficient = -5.91, SE = 1.87]. This suggested that seeds were being quickly removed by *M. surifer*.

DISCUSSION

As expected, our results indicated that rodents were most important in post-dispersal seed removal for the six seed species tested. However, seed removal by all animal types combined, as well as by *Maxomys surifer* alone, did not differ between the two habitat types (evergreen and mosaic) in contrast to our hypothesis.

In our study, compared to the invertebrates, rodents appeared to have a greater impact, removing relatively higher proportions of seeds assigned to the control and removing them faster than invertebrates. On the other hand, invertebrate seed removal resulted in fewer available seeds or made the seeds less desirable for rodents and other vertebrates. Previous studies have found that rodents have influenced plants at all developmental stages (Key et al., 1996). In our experiment, rodent seed removal often took place quickly, except perhaps when the seeds were removed by the some species of ants (e.g., genus *Pheidole*) that were active both during the day and at nights (Dai, personal observation). Seeds dispersed by the gibbons in this study were often scattered as they dropped through the canopy, and were distributed throughout the home ranges of the gibbons. The ability to locate seeds before other competing animals is probably a considerable advantage for rodents in the scramble competition for food resources (Minor & Koprowski, 2015).

The rodent species, *M. surifer* and *L. sabanus* observed removing seeds during our experiment are known as both seed predators and secondary dispersers (Geng et al., 2017,

Table 4. Model-averaged estimates of beta coefficients with standard errors, and *p*-values from candidate models contributing 95% of model weights from 36 sub-models in a binomial regression analysis of seed removal (see Table 3[1] for a description of variables tested).

	Estimate	SE	p
(Intercept)	-1.60	1.68	0.35
Day	0.32	0.76	0.67
Elevation	0.63	0.58	0.28
Mix	-0.02	0.16	0.92
Mosaic habitat	1.38	1.24	0.27
Invertebrates	0.32	0.56	0.57
Rodents	4.23	0.51	<0.001
Rain	0.14	0.24	0.56
<i>I. malayana</i>	-1.30	2.00	0.52
<i>M. horsfieldii</i>	0.40	0.51	0.43
<i>M. tomentosa</i>	-1.93	2.13	0.37
<i>U. lucida</i>	3.81	1.86	0.04
<i>U. rufa</i>	6.85	1.98	<0.001
Treatment	-0.40	0.29	0.17

Yasuda et al., 2000), with rodent secondary dispersers probably having positive effects on seed survival (Corlett, 2017). *Maxomys surifer* is a widespread rodent species, common in many forests of Southeast Asia (Aplin, 2016). The mixed-deciduous forest type dominant in the mosaic habitat in our study site was likely favored by *M. surifer* due to the dense understory; the understory in the evergreen forest and dry-dipterocarp forest were less dense. However, seed removal rates of the two habitat types were relatively even despite the likely higher density of *M. surifer* in the mosaic habitat. This may be due to the considerable proportion (~43%) of mixed-deciduous forest found within the evergreen habitat. Also, while rodents (mostly *M. surifer*) were able to remove seeds within short time periods, it appears that relatively small differences in rodent density between habitat types did not significantly alter seed removal rates. Because using camera images alone cannot determine the fate (consumed or dispersed again) of the seeds removed, tracking of individual seeds is needed to further reveal what happens to the removed seeds.

Both single and multiple species of seeds were found in the gibbon faeces. But having multiple species in an experimental trial did not alter the rate of seed removal. In general however, both rodents and invertebrates exhibited preferences among the six seed species tested. Although *U. rufa* and *U. lucida* were quickly removed by the animals, the two seeds were produced in large quantities which could also be a means to increase the chance of escaping seed predation by granivorous animals (McKone et al., 1998). Species-specific defenses may partly explain preferences shown by the animals and alter their feeding behavior (Fricke et al., 2016). *Microcos tomentosa* was covered by a highly-fibrous endocarp (fruit pulp) tightly attached to the seeds even after the digestion by the gibbons. This trait may render the seeds less palatable to seed predators. By fruiting during the dry season (*M. tomentosa* was found in

November and December), the endocarp might also reduce desiccation throughout the dry season. The leaves of *M. horsfieldii* was found to contain β -caryophyllene (Thang et al., 2013), the main contributor to the spiciness of pepper (Jirovetz et al., 2002). This compound may also exist in the seeds and therefore may also deter predators. In addition, two seed species (*W. robusta* and *M. horsfieldii*) collected in the early rainy season (June–early July) were found germinated soon after defecation. While rodents appear to be less detectable in the late dry and early rainy season (Walker & Rabinowitz, 1992), early germination is probably a plant strategy to escape predation (Yi et al., 2012), perhaps when the abundance of potential predators was lower.

During our study, ants appear to also play an important part in seed removal. Based on the large number of seeds (especially of *U. rufa*) estimated to have been removed by the ants, they are likely the second-most important animal type after the rodents to have an impact on gibbon-dispersed seeds. Seeds removed by the ants maybe carried to various microhabitats, which may render opportunities for seed survival and plant establishment (Vander Wall et al., 2005). The impact of secondary dispersal needs to be investigated using further experimental means, such as treatment cages that can effectively exclude ant access to the seeds.

Seed removal was relatively unaffected by elevation, rainfall and time (day) at which seeds were placed in the field. Variation in elevation in our study site was only 257 m, which was probably too small to cause a significant difference in the experimental results. Seed removal occurred regardless of when the seeds were assigned (day), which indicated a relatively even removal intensity within the experimental period. Since the seeds were placed in the field for relatively long (at least seven days) time periods, we considered this sufficient to consider the seeds as having been exposed to removal (Fedriani et al., 2004). Rodents were shown to visit the sites often during dry periods (periods without rain). This may explain the reduced impact of season on seed removal, such that rodent activity was only reduced during the actual rainfall rather than the entire season.

Further experimental study is needed to separate the impact of rodents from that of invertebrates on overall removal rates. More detailed focus on microclimatic and habitat factors affecting rodent and invertebrates are likely required. A longer-termed study which assesses seasonality and its demographic consequences on these animals will enable a greater understanding of the effects of habitat type.

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