Role of siamang (*Symphalangus syndactylus*) as seed dispersal agent in a Sumatran lowland tropical forest

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Jakarta, Indonesia. Tel./fax. +62-21-4898486, ♥email: farhan.adyn15@gmail.com
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Abstract. *Adyn MF, Sibarani MC, Utoyo L, Surya RA, Sedayu A. 2022. Role of siamang (*Symphalangus syndactylus*) as seed dispersal agent in a Sumatran lowland tropical forest. Biodiversitas 23: 2101-2110.* Seed dispersal is mutualistic interaction between angiosperms and dispersal agents. One of the important dispersers for lowland tropical forests, including in Bukit Barisan Selatan National Park (BBSNP), is siamang (*Symphalangus syndactylus* Raffles, 1821). This study aimed to determine the seed dispersal pattern, composition of dispersed seeds, and the seed fate dispersed by siamangs at Way Canguk Research Station, BBSNP, Lampung, Indonesia, from February-April 2021. We used the continuous focal sampling method to observe siamang behavior, while the purposive sampling method collected feces and seeds. Siamangs dispersed endozoochory dominantly, all fecal contained seeds, deposited more in the morning, and more scattered than clumped. With a gut passage time of 22.5 ± 3 hours, the seed dispersal distance was 223.9 ± 142 meters from the parents. Seeds < 3 mm were more numerous, but seeds > 3 mm were dispersed more often. Siamang was recorded to disperse a mean of 3.3 ± 1.4 species/feces, and 22 species were dispersed. The germination test showed that only 28% of total planted seeds successfully germinated. Based on in situ monitoring, the remaining deposit sites only accounted for 12% of total records, while the germination rate of dispersed seeds from these deposit sites varied. Further studies are needed with a larger sample to test the consistency of these findings.

Keywords: Continuous focal sampling, endozoochory, frugivory, germination, gut passage time

INTRODUCTION

Frugivory by animals usually leads to seed dispersal, which moves seeds away from parent plants (Wang and Smith 2002). Frugivores, particularly vertebrates, play a key role as dispersal agents for most tropical and subtropical plants (Corlett 2017). For example, about 65-95% of woody plant species in Asia tropics and subtropics are dispersed by vertebrates (Corlett 1998). Frugivory also increases the success of seed dispersal by selecting ripe fruit and various seed-handling strategies, e.g., spitting (synzoochory) and swallowing (endozoochory) (Gautier-Hion et al. 1985; Benítez-Malvido et al. 2016).

Primates are considered important seed dispersal agents in tropical forests (McConkey 2018) because primates are about 25-40% of frugivore biomass in these ecosystems (Eisenberg and Thorington 1973; Chapman 1995). To determine the effectiveness of seed dispersers, Schupp (1993) stated that it needs to be measured based on the quantity and quality components. The quantity component of seed dispersal includes the visitation rates and the number of seeds dispersed each time, influenced by disperser abundance and preference (Howe and Smallwood 1982). The quality component is the dispersed seed's survival and germination, determined by seed handling and the deposition quality (Schupp et al. 2010).

Hylobatidae, so-called gibbons, is a primates group smaller in body size than other apes (Hominoidea). The gibbons are highly frugivorous and consume fruits with high sugar and water contents (MacKinnon and MacKinnon 1980; Elder 2009; 2013). They often use figs (*Ficus* spp.) as fallback foods (Marshall et al. 2009). They, including siamang (*Symphalangus syndactylus* Raffles, 1821), are effective seed dispersers in the Asian rainforest (McConkey 2009), consuming many fruits, swallowing a lot of intact seeds, dropping and/or damaging a few seeds, then dispersing the seeds through defecation/feces in their home range (Chivers and Hladik 1984; McConkey 2000; McConkey and Chivers 2007).

Bukit Barisan Selatan National Park (BBSNP) is one of the national parks with the largest remaining lowland tropical rainforest in Sumatra, with around 313,572 ha (WCS-IP 2001). This national park is Sumatra's most distinctive surface structure, with the mountain range stretching from the north end to the south end (Mildawati et al. 2022). The ecosystem requires frugivores, including siamang, to help the seed dispersal process maintain the regeneration of the fruiting plant species in the park (Rusmanto 2001; Atmanto et al. 2014). Siamang is one of the most abundant frugivores in BBSNP (O'Brien and Kinnaird 1996), and one of its population pockets in BBSNP is at the Way Canguk Research Station (WCRS).

Siamang was originally considered true folivores. This statement is supported by the early studies in the Malay Peninsula, suggesting that siamang spend the most time eating on leaves (MacKinnon and MacKinnon 1980). Nonetheless, Elder (2009) evaluated this assumption and clarified that the actual feeding preferences tend to be determined by the fruit availability, mainly figs, in the siamang habitat. According to Nurcahyo (1999), siamangs at WCRS consumed more fruits (52.07%) than leaves (42.62%). Rusmanto (2001) reported that frugivory by siamangs at WCRS generates seed dispersal on 43 species and 88.4% of species are dispersed through endozoochory.

It has been two decades since Rusmanto's (2001) studies and no data updates yet. Therefore, it is necessary to carry out similar research to confirm the latest findings and to add knowledge gaps that have not been revealed, such as the gut passage time and its seed dispersal capacity, to provide deeper insight into the role of the siamangs as a seed dispersal agent. Therefore, this study aimed to determine the seed dispersal pattern, composition of dispersed seeds, and seed fate dispersed by siamangs at WCRS, BBSNP.

MATERIALS AND METHODS

Study period and area

The study was conducted in February-April 2021 at Way Canguk Research Station (WCRS) (5º39'325" South-104º24'21" East), which is in the southern Bukit Barisan Selatan National Park, Lampung, Indonesia (Figure 1). The WCRS area is 800 ha in total, separated by the Way Canguk River into two plot areas, i.e., the northern (200 ha) and southern (600 ha) plots. In each area, there are transverse and longitudinal line transects with a distance of 200 meters between transects. The WCRS area is a habitat for 56 species of 26 mammal families and 207 species of 41 bird families (Iqbal et al. 2001). Furthermore, as a lowland tropical forest (15-70 asl), the WCRS area has more than 420 tree species from 62 families, dominated by dipterocarps (Surya et al. 2020). In addition, there are 32 species from the genus of *Ficus*, which is one group of the key plant species in this ecosystem as a food source for various wildlife (Prabowo 2018).

The WCRS area consists of a mosaic of primary forests, naturally and anthropogenically disturbed forests. The southern area was impacted by the *El Niño-Southern Oscillation* (ENSO) forest fire in 1997, which damaged 165 ha. Furthermore, 7 ha of the northern area was burned in 2015 (Surya et al. 2020).

Procedures

Siamang behaviour observation

Behavioral observations were carried out for 6 weeks using continuous focal sampling (Martin and Bateson 2007) on two adult males and two adult females from two groups of habituated siamangs, namely group S and group G. Adult individuals were chosen as focal subjects because they were assumed to contribute more in seed dispersal rather than the youngster. If the focal subject was unobserved for >10 minutes, the recording was ended. Both home range groups were located in the southern area of WCRS and partly covered the 1997's post-fire area. We followed each focal subject from they are waking up in the morning until resting again in their sleeping tree (the tree used as a sleeping site) in the late afternoon for five consecutive days (the first day was looking for the group, while behavior sampling started next two days in a row for each adult male and adult female), and interspersed two days between groups.
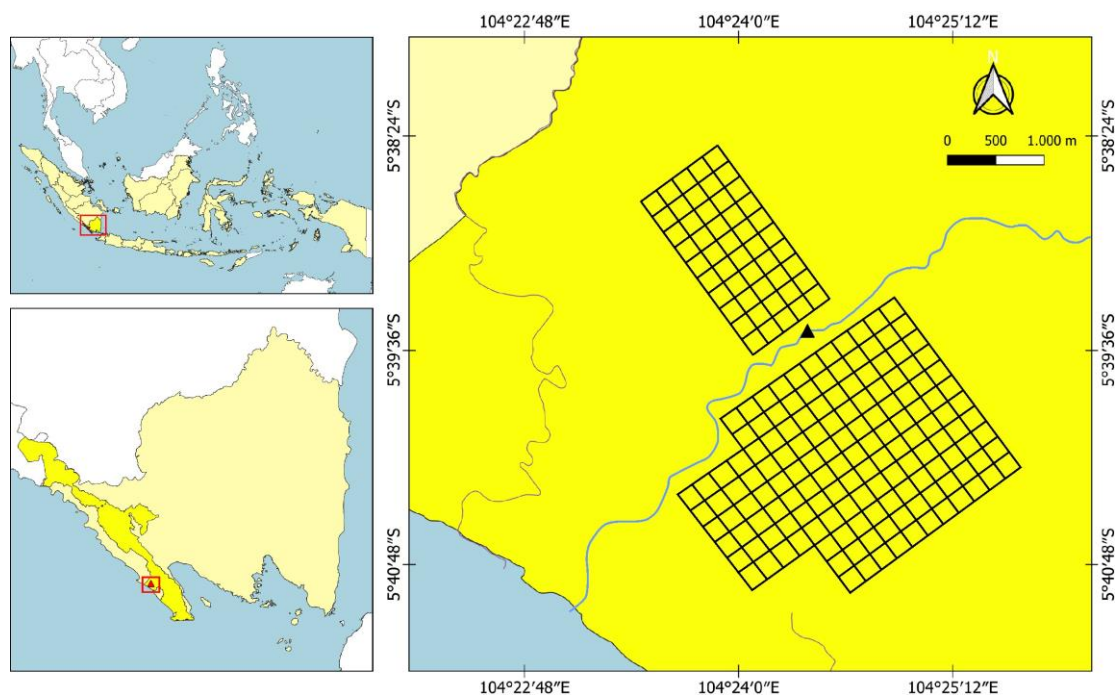

Figure 1. Location of Way Canguk Research Station, Bukit Barisan Selatan National Park, Lampung, Indonesia

The data sampled for seed dispersal analysis were feeding, defecation, and ranging activities. Feeding activity data recorded were feeding location, start and end time, plant species consumed, and food type (fruit, leaves, flowers, or insects). The data recorded in defecation activities were location and time of deposition and amount and condition of the feces (intact/split and dry/wet). Individual positions were recorded every 15 minutes using the GPS unit to determine their daily path length and home range. The *ad libitum* sampling recorded specific behaviors or important seed dispersal events outside the sampling period (Martin and Bateson 2007).

Dispersed seeds collection

When siamangs defecate, half of their feces were collected randomly and filtered for their seed content as fecal seed/ endozoochory samples. Spat seed/synzoochory samples, i.e. seeds that purposively or unintentionally were dropped from discarded fruit or spitted out whole by siamangs, were collected in part and recorded the location and times. If any, seeds that fell naturally to the ground from the parent plant were also collected as uneaten seed samples. The collected seeds were planted in the camp for germination tests, while the rest of the deposited seeds were left embedded and tagged with a tape above the initial deposit site to monitor their seed fate. Each dispersed seed collection was determined by composition, i.e., the number for each species per deposition, and grouped into two size classes (< 3 mm or ≥ 3 mm). Especially for very small seeds (< 3 mm), the number was estimated based on the values of 25 (low), 50 (mid), and 100 (abundant). All data collected from each group were combined and used as group representatives.

Seed fate monitoring

Collected seeds from each handling (fecal/spat seeds) and uneaten seeds (control) were planted in a polybag to conduct a germination test at the day's interval between-group period. Each polybag is filled with soil media used around the camp and planted with five seeds per species per deposit site. Polybags were placed in two semi-open nurseries with a 1.5 x 3 x 1.5-meter size and covered with a shading net. Observations and watering were carried out every day unless it was raining. Before focal subject searches, the initial deposit sites were monitored biweekly in each first day-group group. The state of the dispersed seed, whether it germinated (defined as radicle emergence), still alive/intact, or damaged/dead, was noted. At the same time, canopy openness at each deposit site was measured using Gap Light Analysis Mobile App (GLAMA).

Data analysis
How is the pattern of siamang seed dispersal?

Dispersal mode, date, time, location, and the number of deposited seeds were determined. The gut passage time (GPT) measurement, i.e., the time needed by seeds through the intestine from being swallowed up to being deposited through feces, was carried out to determine the point of the seed parent individual. Each GPT for dispersed seed species is determined by the range (minimum-maximum)

and the average fruit species visited once a day. When the parent and its deposit locations were known, the seed dispersal distance was determined by drawing a straight line from both points. The Spearman's rank test correlation test was performed to determine whether the ranging activity during dispersal is related to dispersal distance. To ensure whether there was a variation that might be due to different conditions of siamang digestive systems that may implicate endozoochory, the defecation frequency, feces number, and GPT of both focal groups were compared using the Mann-Whitney U test.

What is the composition of dispersed seeds?

To determine whether there was a variation caused by differences in the availability of food/fruit sources regarding seed dispersal, both groups' feeding activity budgets and dietary diversity were compared with the Mann-Whitney's test and Hutcheson's t-test, respectively. The number of dispersed seeds was counted and the species was listed. The fruit source's visitation rates and its seed dispersal capacity were determined. To find out whether seed size affects the frequency of seed dispersal events, the Chi-square test was carried out on both focal groups.

How is the post-dispersal seed fate?

The viability rates and germination speeds are determined in the germination test, while the missing planted seeds were not used in the analysis. The survival of dispersed seeds and canopy cover at each deposit site was determined. Spearman's test checks the GPT and shade effect on the dispersed seed's germination probability. The Pearson's test was used to determine whether the dispersal distance is correlated with germination.

All statistical analyses were performed using R 4.0.3 with a significance level of 0.05. The median is presented when data did not normally distribute, while the mean is used otherwise.

RESULTS AND DISCUSSION

Dispersal mode and seeds deposition

Based on 144 seed dispersal events, 93% occurred via feces (endozoochory), while 7% was spat out (synzoochory). In general, siamangs defecated immediately after waking up and shortly after moving from their sleeping tree. This can be seen from the record of the highest defecation activity that occurred in the time range 05:30-06:30 ($N_G = 25$, $N_S = 21$), and tends to decrease in the afternoon and so on (Figure 2a).

The total feces deposited by group G were 428 feces from 114 defecation records, while 460 feces were deposited by group S from 120 records, and the pattern of daily feces deposition was both, as shown in Figure 2b. The number of fecal samples that were successfully collected from group G was 214 samples, while 230 samples were from, and all of these samples contained seeds. The defecation activity and the number of feces deposited of both groups were not significantly different (Mann-

Whitney test t = 0.049, *p* = 0.962; and t = -1.180, *p* = 0.858, respectively).

It was recorded that about 80% of the deposition events by siamangs were spread along the ranging route, while 20% occurred under sleeping trees. There was only one clumping deposit event. The median lag between deposits was 86 meters (N = 192, range 0-448 meters, quartile 41-153 meters), while the median deposition latency was about 70 minutes (N = 192, range 2-566 minutes, quartile 31-114 minutes).

Gut passage time

Based on feeding and defecation activities, it was recorded that 16 individuals of fruit sources from 11 species were only visited once a day by group G and its seeds were found in 75 fecal samples, while group S was recorded to only visit once a day on 16 individuals of 12 fruit species and its seeds were found in 95 fecal samples. Conversely, the 15 individuals from 6 species of fruit sources were recorded to be visited more than once a day by group G and its seeds were found in 54 fecal samples, while 27 individuals from 8 species of fruit were visited more than once a day by group S and its seeds were found in 93 fecal samples. The gut passage times (GPT) for each of these records species are shown in Figure 3.

Overall, there was no difference in GPT between both groups (Mann-Whitney test W = 11,191, *p* = 0.248), with a total mean ± SD of 22.5 ± 3.0 hours, and the median almost the same (median = 22.6 hours for group G, and median = 22.7 hours for group S). Based on the size class of collected seeds, *Embelia ribes* Burm.fil., *Ficus* spp., and *Neolamarckia cadamba* (Roxb.) Bosser belong to the class < 3 mm, while *Antiaris toxicaria* (Pers.) Lesch., *Cananga odorata* (Lam.) Hook.f. & Thomson, *Dracontomelon dao* (Blanco) Merr. & Rolfe, *Garcinia parvifolia* (Miq.) Miq., *Leea indica* (Burm.fil.) Merr., *Mitrephora polypyrena* (Blume) Miq., *Payena acuminata* (Blume) Pierre, *Polyalthia lateriflora* (Blume) Kurz, *Sandoricum koetjape* Merr., *Uvaria* sp., *Vitis* sp., and *Xerospermum noronhianum* (Blume) Blume belong to class ≥ 3 mm. There were differences in GPT within seed size classes (Mann-Whitney test W = 10,193, *p* = 0.019).

Ranging and seed dispersal distance

Based on 46 days of observation efforts and cut off by various obstacles in the field, only 38 observation days were successfully carried out in a full day. The daily path length between both groups was not significantly different (Mann-Whitney test loge(W) = 5.28, *p* = 0.65). The total home range of group G was 24.6 ha (10% covering the post-fire area), while in group S it was 23.4 ha (74% covering the post-fire area).

After the GPT of each fecal seed was matched in the estimation of the time and point when the fruit was first eaten at its deposit site, the median seed dispersal distance (SDD) of group G was 195 meters (N = 129, range 8-445 meter, quartile 108-311 meter), while the median SDD for group S was 225 meter (N = 187, range 2-607 meter, quartile 92-344 meter). There was no correlation between

SDD and the siamang range during dispersal (Spearman test r = 0.04, *p* = 0.393).

Diet and composition of dispersed seeds

Based on 4,055 minutes of total duration, group G spent 65.65% of their time-consuming fruits, followed by leaves by 20.74%, and flowers by 13.61%. The total duration of observation for group S was 4,696 minutes, consisting of 61.68% feeding fruit, 32.67% leaves, and 6.15% flowers. There was no difference in feeding duration between both groups (Mann-Whitney's test W = 75,984, *p* = 0.273). The allocation of individual feeding time for each group is shown in Figure 4.

The fruiting species diversity from the diet of each siamang group was medium ($H_{Gfruits}$ = 2.6; $H_{Sfruits}$ = 2.34), and both were not significantly different (Hutcheson's test t = 0.649, *p* = 0.518). The plant diversity whose leaves were included in both group diets was high ($H_{Gleaves}$ = 3.25; $H_{Sleaves}$ = 3.01), and both were not significantly different (Hutcheson's test t = 1.357, *p* = 0.176). The diversity of flowers on both diets was also medium ($H_{Gflowers}$ = 1.34; $H_{Sflowers}$ = 1.22), but both were also not significantly different (Hutcheson's test t = 0.477; *p* = 0.638). In terms of the overall diet, this indicates that the food composition of both groups is relatively the same and can be analyzed as a single unit.

The visitation rates of fruit sources by siamangs ranged from 2-11 individuals/day or 2-7 species/day. The revisitation of fruit sources was also observed in both groups. Siamang group G used the same fruit source as 40.74% of all individual fruiting plants recorded (N = 54), or 43.98% of all feeding activity records (N = 357), for 2-51 days. Similarly, the number of individual fruiting plants eaten by group S siamangs accounted for 40.74% of all recorded fruiting individuals (N = 54), or 40.64% of all records (N = 406), in the 2-60 days. Both groups often continued to use the same fruit source for days until the availability of ripe fruits was completely depleted, as observed in *A. toxicaria*, *D. dao*, *F. albipila*, *F. altissima*, *F. benjamina*, *F. drupacea*, *F. stupenda*, *G. parvifolia*, *P. acuminata*, *S. koetjape*, *Vitis* sp., and *X. noronhianum*.
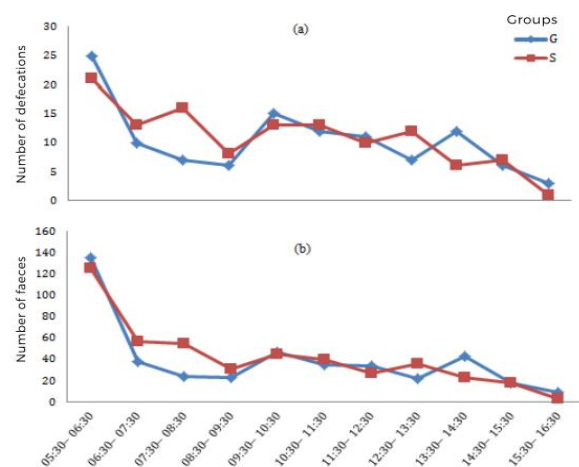

Figure 2. All records of (a) defecation number, and (b) faeces number deposited by each group by time
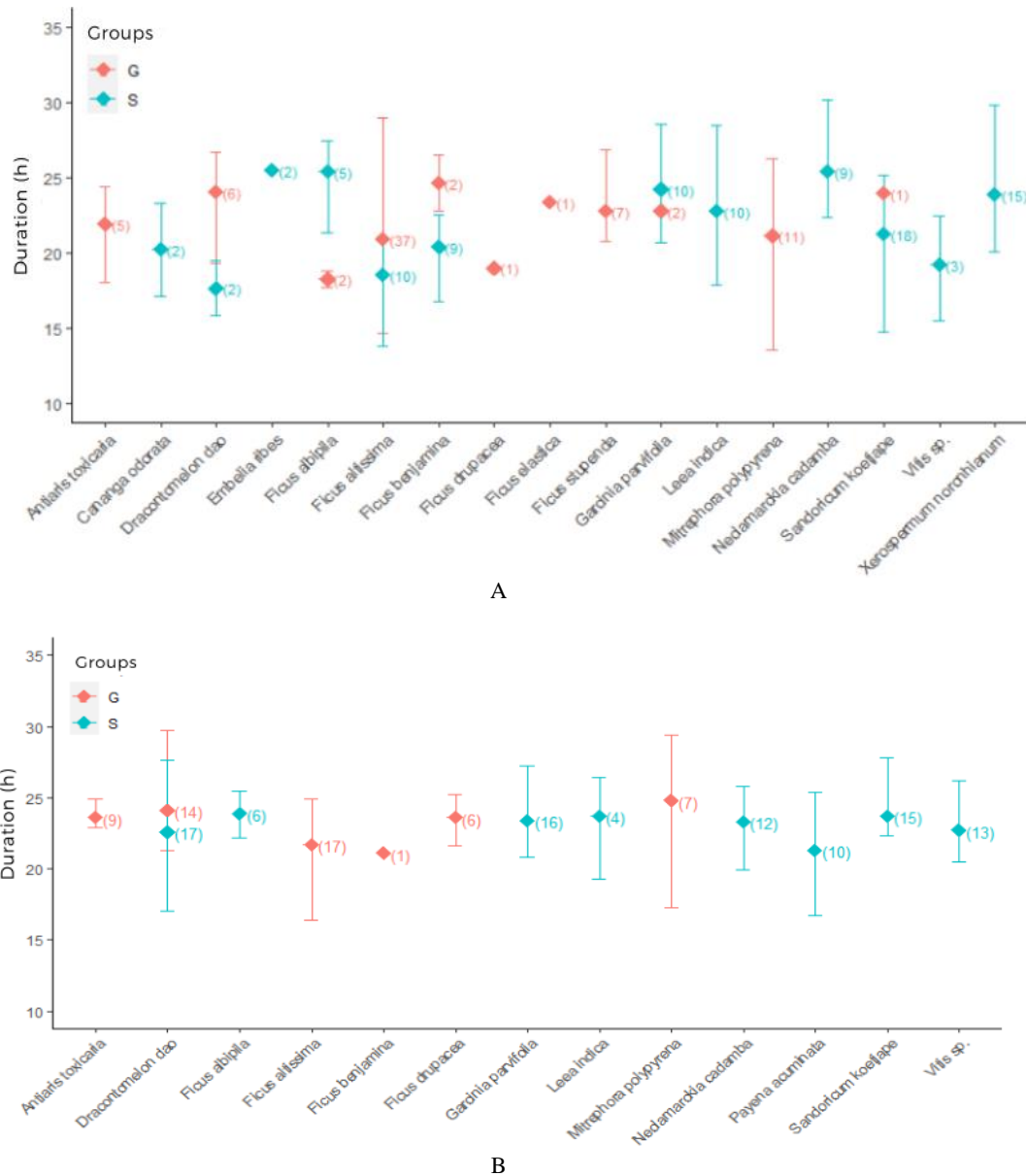
A

B

Figure 3. Mean and range of GPT for (A) each species only visited once, (B) visited more than once a day (numbers in brackets refer to the number of origin faecal samples)
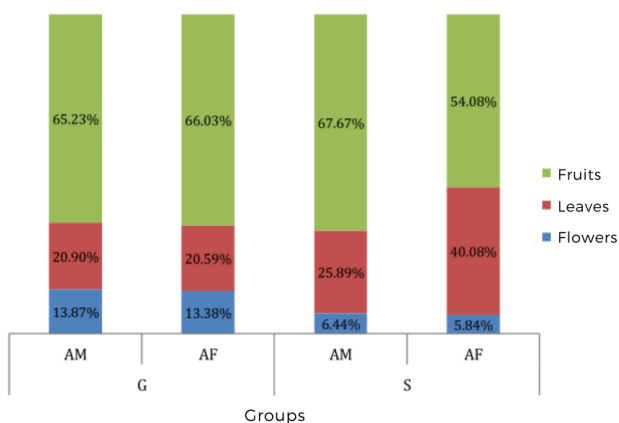

Figure 4. The feeding activity budget spent on different food types

In group G, feces samples were found with a total of 13,831 seeds (12,273 seeds < 3 mm, and 1,558 seeds ≥ 3 mm), while 11,618 seeds in total were found in group S feces samples (9,737 seeds < 3 mm, and 1,881 seeds ≥ 3 mm). Overall, the mean ± SD seeds content per feces was 111 ± 67 seeds (range 3-274 seeds), or 3.3 ± 1.4 species per feces (range 1-8). Notably, *Ficus* spp. and *N. cadamba*, the seeds contained in the feces were very difficult to count because their size is very small (< 3 mm), so the number was estimated. The number of *Ficus* spp. seeds those found in group G feces ranged from 50-9,025 seeds (N_{obs} = 149, $N_{species}$ = 7), while in group S feces it ranged from 1,675-2,100 seeds (N_{obs} = 59, $N_{species}$ = 3). The *N. cadamba* fruits were observed to be consumed only by group S, and about 1,700-4,200 seeds were recorded in the feces (N_{obs} = 90). There was a significant relationship between seed size

classes and dispersal event frequency. However, the proportions in group G were relatively the same, but group S dispersed seeds ≥ 3 mm more often than seeds < 3 mm (Chi-square test X^2 = 51.379, p = 7.616e-13). The frequency of seed dispersal events for all species is shown in Figure 5.

Siamang group S consumed 20 fruiting species and only 16 species were found in feces samples (*A. toxicaria*, *D. dao*, *E. ribes*, *F. albipila*, *F. altissima*, *F. benjamina*, *F. drupacea*, *F. elastica*, *F. stupenda*, *G. parvifolia*, *M. polypyrena*, *P. lateriflora*, *S. koetjape*, *Uvaria* sp., *Vitis* sp., *X. noronhianum*, and *Ficus* seeds which have not been identified), while four fruits species were eaten but the seeds were not found in samples (*F. caulocarpa*, *F. trichocarpa*, *Platymitra macrocarpa* Boerl., and *Siphonodon celastrineus* Griff.). Siamang group G consumed 16 fruiting species, but only 13 seeds species were found in feces (*C. odorata*, *D. dao*, *E. ribes*, *F. albipila*, *F. altissima*, *F. benjamina*, *G. parvifolia*, *L. indica*, *N. cadamba*, *P. acuminata*, *S. koetjape*, *Vitis* sp., and *X. noronhianum*). Three fruiting species were recorded to be eaten by group S, but the seeds were not found in fecal samples (*F. crassiramea*, *F. globosa*, and *Macrosolen cochinchinensis* (Lour.) Tiegh.). Meanwhile, *M. polypyrena* and *Uvaria* sp. are not recorded as being eaten during the observation, but the seeds were found in group S samples.

Germination test

Based on 542 group G faecal seeds planted, it was recorded that 33% were able to germinate, while the germination of group S faecal seeds success was 23% of the 912 seeds planted. The germinated seeds consisted of 11 species for group G and 10 species for group S (Table 1). All the seeds of *F. elastica* and *N. cadamba* that were

planted disappeared, and were not used in the analysis. Because the seed samples for control of each species (uneaten seeds) were limited and not representative enough ($N_{species}$ = 4, N_{seeds} = 14), analysis of the seed handling effect on germination cannot be executed.

Table 1 also shows seeds that did not germinate at all, *C. odorata*, *M. polypyrena*, *G. parvifolia*, and *P. acuminata*. Nevertheless, these species did not mean failure, but there was still a chance to germinate if the observation period was continued. This possibility is indicated as in *E. ribes* and *Vitis* sp., both of which were eaten but only belonged to the S group which germinated because it was recorded that they were dispersed first so that they obtained sufficient observation time. Interestingly, there was a negative correlation between GPT length and the viability of planted dispersed seeds (Spearman test r = -0.14, p = 0.015), meaning that the longer period of GPT the lower viability of dispersed seeds.

Dispersed seeds survival

After being monitored for 3-9 weeks, 10 species were found at the group G deposit site, and 9 species at the group S deposit site remained (Table 2). It was recorded that 48% of the 108 group G deposit sites disappeared, and 52% of the 121 group S deposit sites also disappeared without leaving seeds. The median canopy openness of group G deposit sites was 9.6% (N = 83, range 3.5-26.7%, quartile 7.1-13.6%), and group S median 12.1% (N = 106, range 2.1-39.9%, quartile 8.15-16.2%), while both groups were not significantly different (Mann-Whitney test W = 3.676, p = 0.053). Nevertheless, canopy openness and SDD were not correlated with seed survival or germination probability (Spearman test r = -0.03, p = 0.683; Pearson test r = -0,06, p = 0.821, respectively).
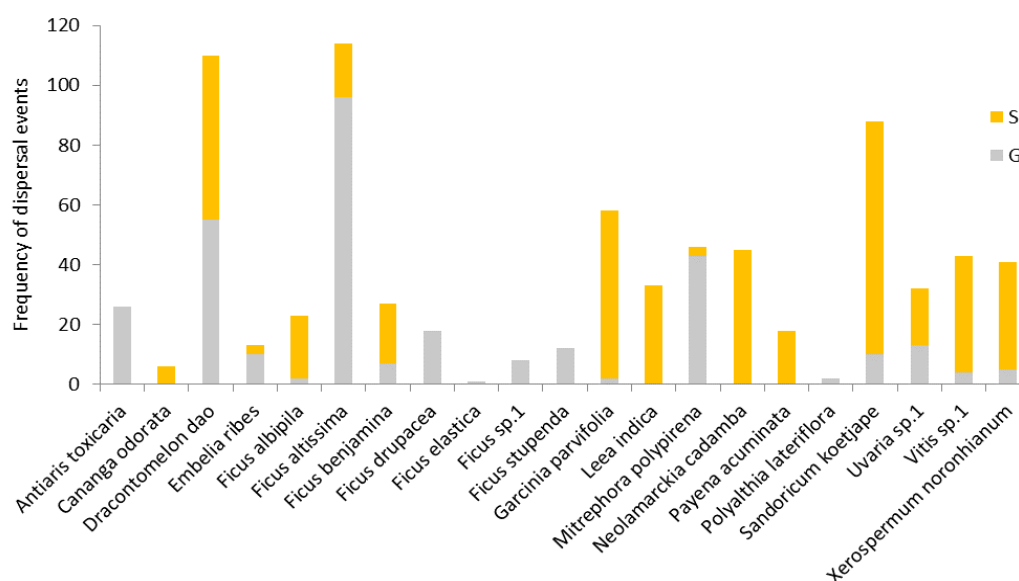

Figure 5. The dispersal events frequency for each dispersed fruiting plants species

Table 1. Germination test of dispersed seeds by each siamang group (N = number of collected seeds planted)

Species	Group G		Group S		Germination speed[1]
	N	Germinated	N	Germinated	
Antiaris toxicaria (Pers.) Lesch.	99	17%	-	-	Early
Cananga odorata (Lam.) Hook.f. & Thomson	-	-	14	0%	Early[2]
Dracontomelon dao (Blanco) Merr. & Rolfe	95	8%	77	6%	Late
Embelia ribes Burm.fil.	13	0%	7	29%	Early
Ficus albipila (Miq.) King	-	-	7	71%	Early
Ficus altissima Blume	142	85%	24	71%	Early
Ficus benjamina L.	5	100%	44	61%	Early
Ficus drupacea Thunb.	17	41%	-	-	Early
Ficus sp.1	4	100%	-	-	Early
Ficus stupenda Miq.	10	80%	-	-	Early
Garcinia parvifolia (Miq.) Miq.	6	0%	213	0%	Delayed[4]
Leea indica (Burm.fil.) Merr.	-	-	111	21%	Early
Mitrephora polypyrena (Blume) Miq.	100	0%	6	0%	Late[3]
Payena acuminata (Blume) Pierre	-	-	18	0%	-[5]
Polyalthia lateriflora (Blume) Kurz	2	50%	-	-	Early
Sandoricum koetjape Merr.	21	19%	216	47%	Early
Uvaria sp.1	14	14%	47	9%	Early
Vitis sp.1	6	0%	90	4%	Late
Xerospermum noronhianum (Blume) Blume	8	25%	38	53%	Early

Note: [1]Based on Garwood (1995): early (< 4 weeks), late (4-16 weeks), and delayed (> 16 weeks); [2]Handayani (2004); [3]Handayani (2019), [4]Ha et al. (1988), [5]Unknown

Table 2. Dispersed seed fate of all remaining deposit sites (N = number of found seeds)

Species	Group G				Group S			
	N	Germinated	Dead	Alive	N	Germinated	Dead	Alive
Antiaris toxicaria	55	44%	0%	56%	-	-	-	-
Cananga odorata	-	-	-	-	4	0%	0%	100%
Dracontomelon dao	50	0%	96%	4%	41	2%	88%	10%
Embelia ribes	13	15%	85%	0%	1	100%	0%	0%
Ficus altissima	64	100%	0%	0%	3	100%	0%	0%
Ficus benjamina	2	100%	0%	0%	1	100%	0%	0%
Ficus sp.1	3	100%	0%	0%	-	-	-	-
Garcinia parvifolia	-	-	-	-	152	0%	96%	4%
Leea indica	-	-	-	-	10	20%	40%	40%
Mitrephora polypyrena	49	8%	20%	71%	1	0%	0%	100%
Payena acuminata	-	-	-	-	7	14%	43%	43%
Sandoricum koetjape	33	0%	94%	6%	219	22%	69%	8%
Uvaria sp.1	22	0%	100%	0%	22	14%	82%	5%
Vitis sp.1	1	0%	0%	100%	7	0%	0%	100%
Xerospermum noronhianum	-	-	-	-	4	50%	0%	50%

Note: Alive: dispersed seeds that have not germinated, are still intact, and not damaged

Discussion

Siamangs predominantly act as seed dispersal agents in endozoochory mode, as is generally done by other hylobatids (Rusmanto 2001; Atmanto et al. 2014; Corlett 2017). Although they use the same sleeping tree frequently, members of the siamang group rarely defecate simultaneously so that the clumping of feces/dispersed seeds is also minimal, but this event may be unavoidable. The high frequency of sleeping trees reused and the high number of feces or seeds deposited increases the clumping chance resulting in highly aggregated seed shadows. It is associated with post-dispersal seed predation rates (Chapman and Russo 2005).

In terms of seed dispersal, movement greatly affects seed deposition. For example, ranging siamangs are often noted to revisit the same fruit source because the ranging route is not one-way but is very oriented towards food sources, as observed in other hylobatids (Chivers 1974; Asensio et al. 2011). This event has the potential to create a certain route that limits the SDD (McConkey and Chivers 2007; Gelmi-Candusso et al. 2019). However, the actual SDD is influenced by home range shape, inhabited habitat type, GPT, and individual behavior (McConkey and Chivers 2007; Phiphatsuwannachai et al. 2018).

According to McConkey (2018), the SDD generated by hylobatids, including siamang in the present study, ranged from moderate to distant (< 1.5 km). *Hylobates muelleri* x *agilis* gibbon has recorded the farthest SDD by hylobatid up to 1.3 km. Still, the average dispersal was often in the 200-400 meter range, and most seeds were dispersed above

100 meters (McConkey and Chivers 2007). Based on a previous study at WCRS, Rusmanto (2001) showed that the mean SDD of each seed species dispersed by gibbons was around 47.6 ± 3.68 meters to 314.6 ± 136.09 meters, while in this study, the mean SDD of all seeds was around 224 ± 142 meter. Atmanto et al. (2014) also reported that siamangs at Way Kanan Resort, Way Kambas National Park, dispersed seeds up to 385 meters. These three findings showed similar results (< 1 km), probably because the characteristics of each population were not much different and were in forests with good canopy continuity and the same habitat type, the Southern Sumatran lowland forest.

The movement of siamang, like other gibbons, is very sensitive to habitat disturbance and is considered to be less able to disperse seeds across different habitat types (Chapman and Russo 2005; Markhamah 2007; Cheyne et al. 2013; McConkey 2018). The across-habitat seed dispersal may only occur if their territory includes a mosaic of habitats and/or large home ranges (Corlett 2017; McConkey 2018; Phiphatsuwannachai et al. 2018; Naniwadekar et al. 2019). This event was observed mostly by the S group because most of the home range and the ranging route covered the post-fire area. The seeds of the parent plant from this area tended to be more often dispersed far > 100 m.

As frugivores, the consumption optimization and high visitation rates of fruit sources demonstrate the importance of certain fruits in siamang's diet to fulfill nutritional requirements. The intensity and frequency of these two activities impact the quantity aspect of the siamang's effectiveness as a seed disperser (Schupp et al. 2010). Differences in food intake between individuals or groups and the fruit sources abundance that are not spread evenly and/or ripen synchronously within each home range cause variations in the number and species of dispersed seeds.

Each planted species for germination tests showed varying success. Even in the same population, seeds from different parents may have different viability or germination patterns (Zalamea et al. 2014). The siamang digestive system, like other gibbons, seems to provide gentle treatment to the seeds, even thin seeds coat or that are bitten and through the intestines are not degraded and both are still able to germinate (McConkey 2000). However, according to McConkey and Chivers (2007), gibbons did not provide a consistent effect on seed germination. Some seeds have a higher germination percentage and faster germination time after passing through the digestive tract than seeds that are not swallowed (Chapman 1995). Still, the longer GPT could remove the mesocarp and damage the seed embryo, reducing viability, particularly for thin-coated seeds (Gardener et al. 1993).

The resilience of the deposit site reflects dispersed seed survival. Deposit sites that did not leave viable seeds occur due to environmental factors (e.g., being washed away by rainwater, crushed by fallen trees, burned, etc.), moved by secondary dispersers, and/or heavily preyed upon seed predators (Vander Wall et al. 2005). The dormancy of swallowed seeds that siamang intestines have not broken

can also affect these findings, mainly for the seeds that germinate slowly/delayed (Garwood 1995).

According to Whitmore (1983), the three most important environmental factors affect the germination of tropical plant seeds: temperature, light, and humidity. These three factors are strongly influenced by the opening formed by the distance between the canopy cover (Raich and Khoon 1990). However, our findings did not show canopy openness correlates to seed germination, which is suspected that the differences in each species' tolerance to shade vary widely. Some species may be very light-dependent for successful germination, while others may grow well in the shade (Dalling et al. 1998). The morphology and physiology of shade-tolerant seeds are highly variable and germinate within months. At the same time, the gap-dependent seeds are also diverse but tend to have a long-dormant period (Dalling 2005).

The Janzen-Connell hypothesis states that dispersed seeds away from the parent plant increase the chance of survival by eliminating density- or distance-dependent mortality factors, and one of the main factors is predation (Connell 1971; Hullman and Kollmann 2005; Janzen 1970), but our results do not verify it. It is assumed that the predation rates of each deposit site vary. For example, Howe et al. (1985) showed fruit/seeds of *Virola surinamensis* (Rol.) Warb. that fell under the parent tree within 12 weeks were found to be almost all dead, while Chapman and Chapman (1996) found that *Uvariopsis congensis* Robyns & Ghesq. experienced 56% seed predation rate more frequently when dispersed away from the parent.

Endozoochory often leaves fecal matter, which attracts seed predators to deposit sites and secondary dispersers (Dalling 2005). However, a secondary dispersal agent plays a vital role and determines the fate of endozoochory seeds, namely the dung beetle (*Scarabaeidae* spp.) (Janzen 1970; Shahabuddin et al. 2005). Any newly defecated feces by siamangs were swarmed by dung beetles immediately. The behavior of dung beetles to move feces containing seeds, by forming feces into balls and then rolling them a few meters from the original deposit and burying them in their deposits, has been shown in several studies to provide an advantage in avoiding seed predators and increasing the survival of the dispersed seeds into seedlings (Beaune et al. 2012). As the interaction gets longer and more intense, secondary dispersal will have implications in seed shadow changes from the initial dispersal pattern by siamang (Chapman and Russo 2005).

The seed dispersal syndrome and behavior of dispersal agents play a significant role before pre-and during dispersal (Gautier-Hion et al. 1985; Flörchinger et al. 2010; Razafindratsima et al. 2018) but are not sufficient to guarantee the post-disperse seed survival (Wang and Smith 2002; Willson and Traveset 2009). In addition to the external factors already mentioned, seed fate is also determined by dispersed seeds' biology. The effect is specific for each species (Chapman and Russo 2005). For example, some plant species not only have a nutritious fruit mesocarp that is often exploited by frugivores, but some of

the seeds are also consumed by seed predators, and an example here is *G. parvifolia*.

The *G. parvifolia* is a dioecious tropical tree that can reproduce apomictically so that its generation is genetically identical to the parent (Ha et al. 1988). Although only a few of its parents were found in both home ranges of the siamang group (Nind = 3), the *G. parvifolia* fruit was one of the siamang's favorite food, and the seeds (≥ 3 mm) were consistently dispersed in large numbers (Figure 5, Tables 1 and 2). Nevertheless, none germinated either in the test or at the deposit site. Moreover, they were often preyed upon and left only the seed coat. Slow germination and high predation rates later determined the regeneration cycle and demography of *G. parvifolia* (Vogel 1980; Richards 1990).

In conclusion, the ability and capacity of siamang seed dispersal suggest their important ecological role in helping the regeneration of fruiting plants, which are also food sources for other wildlife in their habitat. However, the survivability of dispersed seeds is largely determined by various external and internal factors required for successful saplings. Therefore, the study is expected to be a reference for BBSNP managers, researchers, practitioners, and related stakeholders in pursuing in situ siamang conservation strategies, especially to maintain ecological processes and restore their habitat.

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