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Source: Wildlife Biology, 18(1) : 24-34

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/10-049

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Wildl. Biol. 18: 24-34 (2012)
DOI: 10.2981/10-049
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Original article

Seed removal and survival in Asiatic black bear *Ursus thibetanus* faeces: effect of rodents as secondary seed dispersers

Shinsuke Koike, Hideto Morimoto, Chinatsu Kozakai, Isao Arimoto, Koji Yamazaki, Masahiro Iwaoka, Masashi Soga & Masaaki Koganezawa

We investigated the fate of seeds of five tree species hill cherry *Prunus jamasakura*, Korean hill cherry *P. verecunda*, Japanese bird cherry *P. grayana*, giant dogwood *Swida controversa* and crimson glory vine *Vitis coignetiae* in the faeces of the Asiatic black bear *Ursus thibetanus* in a temperate forest in central Japan. Clarifying the fate of seeds dispersed by endozoochorous seed dispersers will enhance assessments of their roles as primary seed dispersers. We established several experimental treatments in the field. Each faeces sample was covered by cages with different mesh sizes which limited accessibility by animals (NM: no mesh, SM: 1 mm mesh and MM: 10 mm mesh). We examined whether seed removal varied among tree species and between mesh-size treatments from 2004 to 2007 (N = 625 samples). We set up an automatic camera trap 1.5 m above the ground at all NM treatments. In the NM treatments, the number of seeds of all tree species decreased immediately after the faeces were set. In June of the following year, < 1% of the seeds from any species remained in the vicinity of the faeces. However, we found 3.0-13.2% intact seeds of all species in the soil below the faeces, as well as within a 10-m radius around the faeces. In the NM treatments, most seed removals were observed within four days after the faeces were set. For all tree species in the MM treatment, most of the seeds were present on the surface of the soil, and 1-2% of the seeds germinated at the location where faeces were set. In the SM treatment, none of the seeds from any of the tree species disappeared and germinated. We took a total of 415 photographs at the NM sites, 97.8% of which were of rodents either holding or eating seeds. Many of the seeds contained in the bear faeces were removed and eaten by rodents. However, 2.1-5.1% of the seeds survived and germinated, which implies that rodents may also act as secondary seed dispersers.

Key words: Asiatic black bear, endozoochory, fleshy fruits, secondary dispersal, seed predation, temperate forest, Ursus thibetanus

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Received 1 May 2010, accepted 3 October 2011

Associate Editor: Daniel Harrison

Along with pollination, seed dispersal is directly related to the reproductive success in plants, and it is one of the few opportunities for plant genes to disseminate. Additionally, the process of seeds being transported away from the parent tree and germinating into new plants in a different location affects the distribution of trees within the forest. Of the numerous mechanisms employed by plants to distribute their seeds, many tree species, which are the principal component species of the forest ecosystem, employ endozoochory. In temperate zones, 50-60% of trees produce fleshy fruit and rely on endozoo-

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chory to disperse their seeds (e.g. Howe & Smallwood 1982, Willson et al. 1989). Studies on mechanisms of seed dispersal have shown that a wide range of animals are involved in endozoochory, including birds, primates and carnivorous mammals (e.g. Jordano 1992, Herrera 2002, Chapman & Russo 2006). Together, the contribution of these frugivores plays an important role in the maintenance and renewal of forests. However, because the different dispersers have different feeding habits and behavioural traits, their efficiency as plant dispersers is also likely to differ (e.g. Jordano et al. 2007, Traveset et al. 2007, Dennis & Wescott 2007).

The efficiency of seed dispersal by animals can generally be defined in terms of qualitative and quantitative efficiency (Schupp et al. 2010). There are two aspects to qualitative efficiency: the degree of damage incurred by the seed as it passes through the gastrointestinal tract of the disperser, and whether the microhabitat of the location where the disperser finally deposits the seed is suitable for germination and subsequent establishment of the seedling. As the qualitative efficiency of different dispersers can be compared relatively easily, numerous studies have investigated this aspect (e.g. Traveset et al. 2007, Koike et al. 2008a,b, Fedriani et al. 2010). However, many of these studies have focused on the first stage of seed dispersal, i.e. removal of the fruit and the range over which the seeds are scattered, and relatively few have examined the second stage, which is the fate of seeds after dispersal (Jordano 1982, Murry 1988, Westcott et al. 2005). Additionally, several studies have examined the relative number of seeds that have been dispersed to safe sites where plant germination and establishment occur (Geritz et al. 1984); however, successful dispersal of seeds does not guarantee successful germination (e.g. Molofsky & Augspurger 1992, Nakashizuka et al. 1995, Ackerman et al. 1996). Often, dispersed seeds are consumed before germination or may be attacked by bacteria or molds (Janzen 1971, Schupp 1988, Chapman 1989). Furthermore, since large mammals may ingest large quantities of fruit during a single feeding event (Koike 2008b), their faeces often contain numerous seeds which may attract seed predators and lead to increased competition among seedlings (Howe 1986, Chapman 1989, Hulme 1993, Pizo & Oliveira 1999, Andresen & Levey 2004). Seeds of endozoochorous species experience high mortality rates resulting from predation and other causes during the interval between egestion from the disperser and the establishment of the seedling; therefore, clarifying the fate of seeds after dispersal is considered to be important within the context of forest management.

Of the studies that have examined the fate of seeds after they have been dispersed by animals, most have been conducted in the tropics (Estrada & Coates-Estrada 1991, Rey et al. 2002, Andresen & Levey 2004, Stephen et al. 2005). Although seeds are removed from faeces by weathering (e.g. wind or rain) and biotic factors, it is unlikely that all the seeds will disappear in this way (Crawley 1992). Biotic factors include the action of rodents, ants or dung beetles (Janzen 1982, Estrada & Coates-Estrada 1991, Pizo & Oliveira 1999, Andresen 1999, Gross-Camp & Kaplin 2005), which can have substantial effects on the fates of seeds. Although rodents can act as secondary dispersers of seeds through hoarding food, they are considered to have their greatest effects as seed predators (Bond & Breytenbach 1985, Forget 1990, 1991, 1996, Janzen 1982, Galetti et al. 1992). Ants are often responsible for the movement of seeds of particular plants species and the action of transporting the seeds can facilitate germination (Horvitz & Schemske 1986, Hughes & Westoby 1992, Benett & Krebs 1987). Dung beetles rely on faeces for food and have also been implicated in the secondary movement of seeds when they transport faeces containing seeds underground (Andresen & Feer 2005). These biotic factors are commonly associated with defaecation by frugivorous mammals (Willson 1993), and the existence of seed predators and secondary dispersers is considered to have an enormous impact on the survival of the seeds that are dispersed by mammals (e.g. Chapman 1989).

It seems reasonable to expect larger frugivorous mammals to consume a wider range of fruit species than smaller animals (Mack 1993), and larger animals are more likely to disperse these seeds over a relatively wider area (Campos-Arceiz et al. 2008). Bears (Ursidae) are distributed from tropical areas to polar zones, they feed on fruits (Narita et al. 2006) and are known to act as seed dispersers in a variety of ecosystems (Traveset & Willson 1997, McConkey & Galetti 1999, Auger et al. 2002, Willson & Gende 2004, Takahashi et al. 2008, Koike et al. 2008a). Indeed, because of their enormous capacity for movement, bears have been implicated in the dispersal of seeds over extensive areas (Willson 1993, Koike et al. 2011). However, because of the high density of seeds in bear faeces, undisturbed bear faeces may not favour the germination of seeds or the establishment of seedlings (Koike et al. 2008b). Bears

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are considered to have both positive and negative effects on qualitative dispersal processes. Since relatively few studies have examined the fate of such seeds in bear faeces (see Bermejo et al. 1998, Sreekumar & Balakrishnan 2002), we conducted our study to clarify seed fate in the faeces of Asiatic black bear *Ursus thibetanus* in temperate forests of Japan.

Clarifying the fate of seeds dispersed by endozoochorous seed dispersers may enhance our understanding of their roles as primary seed dispersers. In this study, we tracked the fate of seeds after dispersal by bears with the goal of estimating both seed removal and survival using marked seeds. Specifically, we examined the effectiveness of bears as seed dispersers by determining: 1) which species affected the fate of seeds contained in bear faeces, 2) whether the species that consumed seeds in bear faeces functioned as secondary dispersers or solely as seed predators, and 3) whether any of the seeds dispersed by bears actually germinated.

Material and methods

Study area

Our study was conducted in the Mine area in the town of Okutama, approximately 100 km west of Tokyo, Japan. The climate of the study area is typical of areas along the Pacific Ocean, with heavy rainfall in summer and little snow in winter. The mean annual precipitation is 1,586 mm, mean snowfall ranges from two to four cm, and the mean annual temperature was 11.8°C during 2005-2006, ranging from 0.6°C in January to 24.2°C in August (Tokyo Environmental Office 2006).

The mountainous area is mostly covered by natural forests and conifer plantations of Japanese cedar *Cryptomeria japonica* or Japanese cypress *Chamaecyparis obtusa* covering 41.3 and 50.3% of the area, respectively. Natural forests at the lower altitudes (400-500 m a.s.l.) are dominated by Japanese chestnut *Castanea crenata* and Japanese white oak *Quercus serrata*, with areas in the middle altitudes (500-1,500 m a.s.l.) dominated by Japanese oak *Q. crispula,* Japanese chestnut and Japanese beech *Fagus crenata*, and the upper altitudes (1,500-1,800 m a.s.l.) dominated by Nikko fir *Abies homolepis* and Northern Japanese hemlock *Tsuga diversifolia*. Our study area was located in a Japanese oak-Japanese chestnut community at the middle altitudes of 800-1,200 m a.s.l.

Selection of plant species

Asiatic black bears *Ursus thibetanus* in Japan have been reported to feed on a wide variety of fruits during June-November (Koike 2009). Of these, in our study, we considered fruits of five tree species in the vicinity of the study area (Koike et al. 2008b), including hill cherry *Prunus jamasakura* (fruiting period in June and seed diameter of 6.5 mm), Korean hill cherry *P. verecunda* (July; 6.8 mm), Japanese bird cherry *P. grayana* (August; 6.1 mm), giant dogwood *Swida controversa* (September; 5.4 mm) and crimson glory vine *Vitis coignetiae* (October; 4.8 mm; Koike 2009, Koike et al. 2011).

Fate of dispersed seeds

Preparation of seeds and artificial faeces

As it is not possible to collect bear faeces containing a known quantity of seeds under natural conditions, bear faeces were artificially combined with a known quantity of seeds ('experimental faeces'). Prior to the experiment, fruit from each of the plant species examined was fed to bears kept at the Institute of the Japanese black bear in Ani Akita, Japan. We collected faeces and removed the seeds and the faeces were frozen until commencement of the experiment. We maintained intact seeds collected from faeces at cool (5°C) and dry (humidity $< 15\%$) conditions (Ishii 1991) until the experiment. We marked the endocarps of all seeds used in the experiment using scentless paint, which enabled us to determine how many seeds were removed from the treatments or how many seeds germinated by observing remains from marked endocarps.

For field experiments, we prepared simulated faeces by mixing 100 g of bear faeces with 100 marked seeds that had passed through bears for each of the plant species. Seeds were mixed into the faeces in the same proportion (seeds/unit weight of faeces) as faeces collected in the field.

Experimental design

We developed five treatments for field experiments. We used simulated faeces in all treatments, except in the non-faeces (NF) and in the controls (C) of the experimental treatments where seeds were placed without faecal material. The mesh used in the medium mesh (MM) and small mesh (SM) treatments consisted of a hemisphere measuring 60 cm in diameter and 30 cm high, positioned with the point of the cone pointing upward and the bottom end buried to a depth of approximately 20 cm. The experimental treatments were as follows:

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No mesh (NM) treatment: Experimental faeces set on the floor of the forest, not surrounded by mesh;
MM treatment: Experimental faeces set on the floor of the forest, surrounded by 10 mm mesh. Mesh size was selected considering the skull size of rodents as described in Oh et al. (2003). It was assumed that rodents could not enter this cone;
SM treatment: Experimental faeces set on the floor of the forest, surrounded by 1 mm mesh. Mesh size was selected considering the size of dung beetles, and it was assumed that dung beetles could not enter this area (Kawai et al. 2005);
NF treatment: Only marked seeds set on the forest floor. The purpose of this treatment was to clarify the presence of faeces on seed fate;
C treatment: Unmarked seeds only set on forest floor. The purpose of this treatment was to clarify whether marking affected seed fate.

We established 100 × 100 m grids and placed a simulated faeces or seeds (NF and C treatments) at a site that was equally spaced 50 m from the closest adjacent faeces or seeds.

We prepared 25 simulated faeces for each plant species with five replicates for each of the five treatments (NM, MM, SM, NF and C), which yielded a total of 125 simulated faeces or seed clusters (NF and C) that were established for each species and 625 simulated faeces or seed clusters (NF and C treatment) across all of the five tree species evaluated. We established the treatments during the fruiting period of each plant species; hill cherry, early June 2004; Korean hill cherry, early July 2005; Japanese bird cherry, mid-August 2006; giant dogwood, early September 2007; and crimson glory vine, early October 2004.

We observed marked seeds on five occasions after the simulated faeces were set at intervals of two and four days, one week, one month and then once again in June of the following year. Each simulated faeces or seed group (NF and C treatments) was observed only once.

During each observation, we assessed five experimental faeces from each treatment and counted the number of intact, marked seeds in the area immediately surrounding the faeces (area A, defined as the surface of the soil in a 30-cm radius from where the faeces was originally set). In the observation performed in June of the following year, we examined three different areas except C: the area around the faeces (area A), the soil under the faeces (area U; defined as the soil below the faeces to a depth of 20 cm within a 30-cm radius of the faeces) and the area surrounding the faeces (area S; defined as the soil to a depth of 5 cm within a 10-m radius of the faeces, excluding areas A and U). Our observations not only included seeds with marked endocarps, but also the marked endocarps in instances where seedlings had emerged from marked seeds. Additionally, when marked seeds had been preyed upon, we estimated the number of seeds based on the remaining seed fragments. The number of damaged seeds was a conservative estimate based on visual observations of endocarp damage and did not include intact seeds.

Camera trap placement

An automatic camera trap (Fieldnote, Marifu Co. Iwakuni City, Japan) was set up 1.5 m above the ground surface at each NM treatment. We set up five cameras to evaluate each tree species, and the results were pooled for the total of 25 cameras. Cameras were operated for a two-week period after experimental faeces were set.

Statistical analysis

In order to test the following seven questions, we compared treatments at every observation by Bonferroni type pairwise t-tests. Bonferroni correction sets the alpha value for the entire set of n comparisons equal to α by taking the alpha value for each comparison equal to α/n. First, to evaluate the effect of seed marking on rates of seed disappearance, we compared NF (no marked seeds) and C (marked seeds) treatments. Second, to evaluate the effect of faeces on the seed disappearance, we compared NF (seeds with no faeces) and NM (seeds with faeces) treatments. Third, to examine the effect of faeces on the seed disappearance after one year (area A), we compared NF and NM treatments for the next year again. Fourth, to examine the effect of dung beetles and rodents on seed burial under the ground (area U), we compared NM (both dung beetles and rodents can bury seeds) and MM (only dung beetles can bury seeds) treatments for the next year. Fifth, to examine the effect of faeces on seed removal from the surrounding area (area S), we compared NM (seeds with faeces) and NF (seeds with no faeces) treatments for the next year. Sixth, to examine the effect of dung beetles and rodents on seedlings around the faeces (area A), we compared NM (both dung beetles and rodents can bury seeds) and MM (only dung beetles can bury seeds) treatments for the next year. Seventh, to examine the effect of faeces on seedlings in the area surrounding the faeces (area S), we compared NM

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(seeds with faeces) and NF (seeds with no faeces) treatments for the next year. In our study, patterns of seed disappearance were not different among the five plant species (Fig. 1); thus, we pooled these plant species in later analyses. We conducted all of the analyses using the R software package (version 2. 12. 0, R Development Core Team 2003).

Results

During the experimental period, we observed no instances where the mesh or faeces had been trampled on, dug up or otherwise disturbed by animals. In addition, with the exception of the crimson glory vine seeds (in October), most of the faeces residues had disappeared within 10 days after being set on the ground in the SM treatment, and within four days in the NM and MM treatments. In the SM treatment, none of the seeds of any of the plant species had disappeared and even germinated after one year (see Fig. 1). In the MM treatment, the disappearance of seeds on the ground from all species was observed only two and four days after the faeces were set; thereafter, we observed no further changes in either the MM or SM treatments (see Fig. 1).

Seed disappearance during the first month

First, to evaluate the effect of marking on seed disappearance, we compared the rate of seed disappearance in the NF and C treatments and observed no significant differences in any of the four observations after two days, four days, one week and one month (all N (C)=25, N (NF)=25; two days: t=2.12, four days: t = 0.11, one week: t = 0.83, all P = 1.00), indicating that marking had no effect on seed disappearance. Therefore, we removed the data of C treatment from further analysis. Secondly, we compared the NF and NM treatments to evaluate the effect of faeces on seed disappearance and found significantly greater disappearance rates for seeds in the NM treatments after two days, four days and one week (two days: t = 15.18, four days: t = 25.78, one week: t=10.94; all N (NM)=25, N (NF)=25; all P < 0.001). However, one month or more after the treatments were set up, the rate of disappearance was not significantly different between the NM and NF treatments (one month observation, N (NM) =

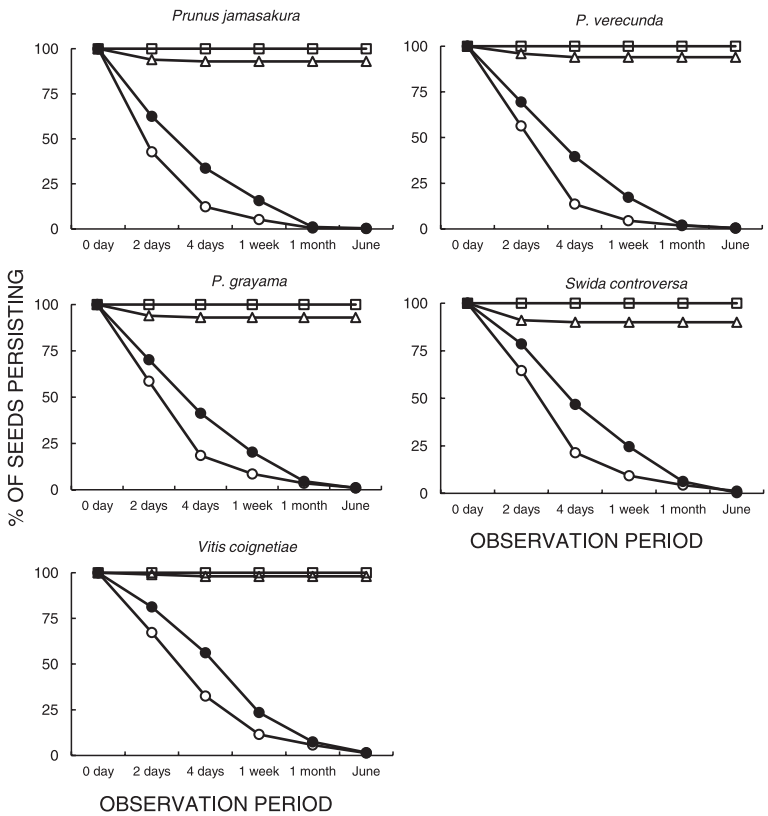


Figure 1. Percentage of seeds persisting for five tree species among no mesh (NM; ○), no faeces (NF; ●), medium mesh (MM; △) and small mesh (SM; □) treatments. June indicates the observation conducted one year after the faeces samples were set.

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Table 1. Percentage (mean ± SD range) of seeds and seedlings, pooled for all species, observed in areas around the site of faeces deposition one year after setting in NM, MM, SM and NF treatments. The area symbols are A, around faeces on the ground; U, soil below the faeces to a depth of 20 cm within a 30-cm radius of the faeces and S, soil to a depth of 5 cm within a 20-m radius of the faeces, excepting areas A and U.

		Treatment			
Condition	Area	NM	MM	SM	NF
Intact	A	0.4 ± 0.6 (0 - 2)	93.8 ± 3.4 (85 - 100)	100	0.9 ± 1.0 (0 - 4)
	U	2.5 ± 3.2 (0 - 11)	4.9 ± 3.7 (0 - 11)	0	0
	S	4.6 ± 4.4 (0 - 12)	0	0	2.8 ± 2.1 (0 - 8)
Seedling	A	2.1 ± 2.3 (0 - 7)	1.4 ± 1.3 (0 - 4)	0	0
	S	3.7 ± 3.8 (0 - 11)	0	0	2.4 ± 1.5 (0 - 6)
Disappearance		21.1 ± 15.6 (5 - 45)	0	0	21.1 ± 17.4 (4 - 41)

25, N (NF) = 25; t = 1.29, P = 1.00), as illustrated for the individual species in Figure 1.

Seed disappearance and seedlings during next year

When we examined the seeds of all species in June of the following year, we observed almost no intact seeds on the soil surface (area A) in the NM (nine of 2,500 seeds) and NF treatments (23 of 2,500 seeds; Table 1). In the area U, intact seeds only existed in the NM and MM treatments, and the number of seeds in the area U was not significantly different between NM and MM treatments (N (NM) = 25, N (MM) = 25, t = 2.31, P = 0.97; see Table 1). In the area S, intact seeds were only found in the NM and NF treatments, and the number of seeds at NM treatment was not significantly higher than NF treatment (N (NM) = 25, N (NF) = 25, t = 1.63, P = 1.00; see Table 1).

In area A, seedlings from marked seeds were found only in the NM and MM treatments, and the number of seedlings was not significantly different (N (NM) = 25, N (MM) = 25, t = 0.68, P = 1.00; see Table 1). In the area S, seedlings from marked seeds were only found in NM and NF treatments, but there was no difference in the number of seedlings (N (NM) = 25, N (NF) = 25, t = 1.29, P = 1.00; see Table 1). In total, 12.5-30.5% of marked seeds from all species were unaccounted for in the NM treatment (mean ± SD 12.5 ± 13.3%; hill cherry, 15.9 ± 16.1%; Korean hill cherry, 24.3 ± 19.4%; Japanese bird cherry, 25.4 ± 18.3%; giant dogwood and 30.5 ± 28.6%; crimson glory vine).

Camera trapping in the NM treatments

In the NM treatment, the automatic camera traps took an average of 327 photographs of vertebrates

Table 2. Total number of photographic events by camera stations in the NM treatment for five tree species. Numbers in parentheses indicate the percentage of photographs containing vertebrates. Only for *Apodemus* species, photographs confirmed that they had seeds in their mouth or carrying seeds away.

Species	Hill cherry		Korean hill cherry		Japanese bird cherry		Giant dogwood		Crimson glory vine	
Apodemus speciosus	314	(92.6)	279	(86.1)	286	(84.4)	323	(90.2)	252	(91.6)
Apodemus argenteus	14	(4.1)	19	(5.9)	26	(7.7)	31	(8.7)	13	(4.7)
Apodemus spp.	5	(1.5)	13	(4.0)	22	(6.5)	2	(0.6)	5	(1.8)
Apodemus total	333	(98.2)	311	(96.0)	334	(98.5)	356	(99.4)	270	(98.2)
Turdus cardis	4	(1.2)	5	(1.5)	1	(0.3)	0	(0.0)	0	(0.0)
Garrulus glandarius	2	(0.6)	8	(2.5)	4	(1.2)	2	(0.6)	0	(0.0)
Meles meles	0	(0.0)	0	(0.0)	0	(0.0)	0	(0.0)	5	(1.8)
Unknown	14	(4.1)	16	(4.9)	12	(3.5)	14	(3.9)	19	(6.9)
Apodemus with seeds in their mouths	80		65		90		55		90	
Apodemus carrying seeds away	50		40		45		60		80	
Number of photographs of no vertebrate	81		73		63		70		79	
Number of photographs of vertebrate	339		324		339		358		275	
Total number of photographs	434		413		414		442		373	
Number of camera stations	5		5		5		5		5	

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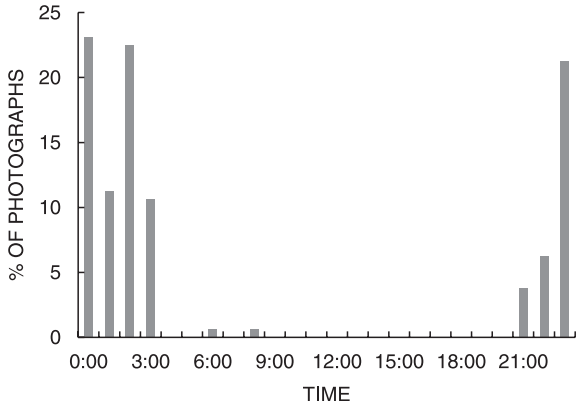


Figure 2. Diurnal patterns of visitations to simulated bear scats by rodents at the no mesh (NM) treatment for five seed-producing tree species as verified by automatic camera traps.

(339; hill cherry, 324; Korean hill cherry, 339; Japanese bird cherry, 358; giant dogwood and 275; crimson glory vine) during the two-week period after the experimental faeces samples were set. Rodents such as large Japanese field mouse *Apodemus speciosus* and small Japanese field mouse *A. argenteus*, badgers *Meles meles*, jays *Garrulus glandarius*, copper pheasants *Syrmaticus soemmerringii* and Japanese thrushes *Turdus cardis* were photographed, with rodents accounting for 97.8% (N = 333; hill cherry 311; Korean hill cherry 334; Japanese bird cherry 356; giant dogwood and 270; crimson glory vine) of the photographs (Table 2). Of the rodent photographs, > 95% were taken between sunset and sunrise, and rodents were photographed eating seeds, holding seeds in their mouths or carrying seeds acquired from the faeces (Fig. 2). Approximately 70% of the photographs of rodents were taken within three days of the faeces being set (Fig. 3). We documented an average of 76 photographs of rodents with seeds in their mouths (76 hill cherry; 65 Korean hill cherry; 90 Japanese bird cherry; 55 giant dogwood and 90 crimson glory vine), and an average of 55 photographs of rodents carrying seeds away (55 hill cherry; 40; Korean hill cherry; 45 Japanese bird cherry; 60 giant dogwood and 80 crimson glory vine; see Table 2). We could not confirm, however, whether other vertebrates documented in photographs had seeds in their mouths.

Discussion

We clarified the fate of seeds dispersed by endozoochorous seed dispersers using an experimental approach with marked seeds. In the following, we address each of the research questions asked.

Seed predators and seed dispersers

Which species affected the fate of seeds contained in bear faeces, and did these species act as secondary dispersers or solely as seed predators? Of the seeds, > 90% contained in the bear faeces were removed by rodents. However, these rodents may not only act as seed predators, but also as secondary dispersers through their food-hoarding behaviour, as suggested by photographs of rodents carrying seeds away from sites where faeces were set.

Even in the SM treatment, which would have been inaccessible to most organisms, the faeces had disappeared after approximately 10 days, implying that decomposition could be attributed to the action of bacteria, small organisms in the soil and weathering. Interestingly, unless mammals were present,

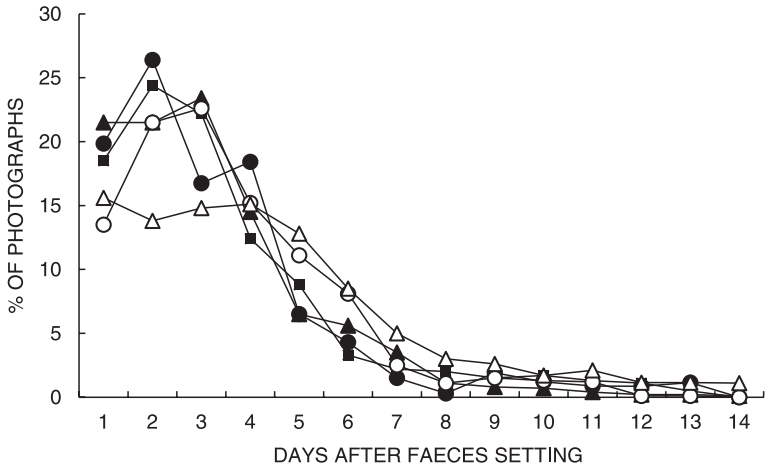


Figure 3. Percentage of photographs containing rodents in the no mesh (NM) treatment as related to time since simulated faeces were set. Symbols represent hill cherry (●), Korean hill cherry (■), Japanese bird cherry (▲), giant dogwood (○) and crimson glory vine (△).

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no substantial movement of the seeds or germination was observed in any of the treatments. In the NM treatment, many of the seeds in the faeces disappeared within 1-4 days, or only the endocarp remained. Of the photographs taken by the automatic camera, > 90% were of rodents, mainly at night. The photographs revealed that a variety of vertebrates, mostly rodents, are the first to appear at bear faeces, implying that the seeds contained in the faeces of frugivores are an important food sources for seed eaters (Willson 1993). In general, finding a large concentration of seeds in one place is unusual, which is probably why almost all of the seeds in the NF treatment disappeared, albeit at a slow rate, within one month of the seeds being set. Future work into the contribution of rodents on seed fate will need to examine the value of the seeds within fallen fruit and faeces as food sources for rodents.

We observed seed movement around the faeces in the MM treatment, which was accessible to only insects. Previous studies in the tropics have shown that dung beetles affect seeds contained in faeces (Estrada & Coates-Estrada 1991, Andresen & Feer 2005). It is possible that some of the seedlings found around the faeces were derived from seeds buried by dung beetles. In the future, the role of dung beetles should be studied in temperate forests.

Germination of seeds dispersed by bears

Previous studies from tropical areas have also shown that the presence of rodent seed predators greatly affects the survival of seeds after dispersal (Janzen 1982, 1986, Willson 1989, Andresen 1999), as also found in our study. It should be noted, however, that 3.7% of our experimental seeds were recovered as seedlings in the area surrounding the faeces (area S), suggesting that hoarding by rodents may result in some secondary dispersal of seeds. Seedlings were interspersed with consumed seeds (endocarps) suggesting that not all seeds that were carried away by rodents were consumed. Masaki et al. (1998) also indicated that rodents hoard the seeds of fleshy fruits, and rodents hoarding walnuts *Juglans ailanthifolia* moved the seeds approximately 30-50 m (Tamura et al. 2005). Indeed, it is possible that the 21.1% of seeds that could subsequently not be accounted for (see Table 1) may have been spread over a wider area. It is also possible that these seeds were buried deep in the ground, in which case their chances of germination would have been reduced. Nonetheless, secondary dispersal by rodents has been shown to result in seeds being buried in soil and in other areas (Forget et al. 1998, Vander Wall & Joyner 1998), and it is likely that covering the seeds with soil would increase their chances of germination.

Conclusions

Bears can disperse several thousands of seeds in a single scat (Koike et al. 2008b); therefore, they are potentially very important seed dispersers. However, such high concentrations of seeds also have a high risk of predation. The observations in our study confirm that rodents prey extensively on seeds contained in Asiatic black bear faeces, and also that some seeds survive and germinate, which suggests that the rodent predators may also act as secondary dispersers of seeds. Because we did not collect comparable quantitative data for other dispersal agents, and did not document how many seeds would have germinated without being consumed by bears, we were unable to evaluate how phenomena besides rodent predation affected the effectiveness of seed dispersal by bears. Also, we did not determine whether the rodents actually increased or decreased the ultimate reproductive success of the parent tree.

Acknowledgements - we wish to thank K. Furubayashi for valuable comments and discussions related to our study. We also thank the many people who helped us in the field, particularly S. Kasai, Y. Goto, T. Komatsu and M. Suzuki, who provided useful advice regarding the feeding trials at Ani. We also extend our gratitude to H. Ueda, T. Masaki and A. Nakajima for their helpful advice. Lastly, we thank the reviewer P.M. Forget, Associate Editor D. Harrison and Editor-in-Chief I. Storch for their help in improving the content and readability of the manuscript. This study was partly funded by a Grant-in Aid for JSPS Fellows (No. 20880012) and the Tokyu Foundation for better Environment.

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