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ORIGINAL RESEARCH

Seed dispersal function of the brown bear *Ursus arctos* on Hokkaido Island in northern Japan: gut passage time, dispersal distance, germination, and effects of remaining pulp

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Abstract

Megafauna are important seed dispersers because they can disperse large quantities of seeds over long distances. In Hokkaido, Japan, the largest terrestrial animal is the brown bear (*Ursus arctos*) and other megafauna seed dispersers are lacking. Thus, brown bears are expected to have an important function as seed dispersers in Hokkaido. In this study, we, for the first time, evaluated the seed dispersal function of brown bears in Hokkaido using three fleshy-fruited trees and studied: (1) gut passage time (GPT) in feeding experiments, (2) seed dispersal distance using tracking data of wild bears, and (3) the effect of gut passage and pulp removal on germination rate. Most seeds were defecated intact, and less than 6% were broken. The average GPT without pulp was 3 h and 56 min to 6 h and 13 min, depending on the plant and trial. Each plant's average simulated seed dispersal distance was 202–512 m. The dispersal distance of *Actinidia arguta* seeds with pulp was significantly longer than those without pulp because of their longer GPT. The germination rate of defecated seeds without pulp was 19–51%, depending on the plant, and was significantly higher or not different comparing with that of seeds with pulp. We concluded that brown bears in Hokkaido are effective seed dispersers. In managing brown bears in Hokkaido, such ecological functions should be considered along with conserving the bear population and reducing human–bear conflicts.

Keywords Endozoochory · *Padus grayana* · *Vitis coignetiae* · *Actinidia arguta* · Megafauna

Introduction

Endozoochory (seed dispersal via animal ingestion) is common in ecosystems worldwide (Dennis et al. 2007; Jordano 2014; Travset 2014). Megafauna dispersers (dispersers with large body sizes) can potentially disperse large quantities of seeds (> 1000 seeds in a scat; Shakeri et al. 2018; García-Rodríguez et al. 2021a) over long distances (> 10 km; Corlett 2009). Consequently, they significantly impact the distribution and demography of the dispersed plants. However, many megafaunal species are endangered because they often require large natural habitats without severe human disturbances (Ripple et al. 2015, 2017). An extinction or decline in the population of megafauna dispersers affects plant demography and evolution (Gardner et al. 2019; Rogers et al. 2021). For example, the local extinction of megafauna dispersers in the forests of Southeast Asia due to hunting increases the extinction risk of plant species (Caughlin et al. 2015); seed dispersal distances by emu (*Dromaius novaehollandiae*) shortened when habitat loss and fragmentation increased (Nield et al. 2019), and a global-scale meta-analysis revealed that the ability of plants to track climate change has been lost due to the loss of dispersers, including megafauna (Fricke et al. 2022). Therefore, megafauna is particularly important for conserving the ecological functions of seed dispersal.

The brown bear (*Ursus arctos*) is one of the largest terrestrial animals in the temperate and subarctic zones. Previous studies have revealed some aspects of seed dispersal by brown bears, such as fruit diet (García–Rodríguez et al. 2021a), gut passage time (GPT) (Elfström 2013), dispersal distance (Lalleroni et al. 2017), and germination rate (Traveset and Willson 1997; Willson and Gende 2004; García-Rodríguez et al.

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2021b), indicating that brown bears are effective seed dispersers. These studies have also indicated that dispersal interactions differ depending on the population, reflecting variations in body size, diet, and habitat use (Haroldson et al. 2020; Swenson et al. 2020). However, to our knowledge, no studies have investigated the entire dispersal process, from feeding to germination, by focusing on the same bear population and plant species.

The study site Hokkaido is an island located in the northmost part of Japan (41art–45art N, 139rt of Japan E; 77,984 km^2). The largest terrestrial animal on the island is the brown bear (Ohdachi et al. 2009). Brown bears on the island have been isolated from other continental bear populations. The maximum recorded weights were 400 kg for males and 152 kg for females (Ohdachi et al. 2009). Candidates of the second-largest seed dispersers in Hokkaido are the raccoon dog (*Nyctereutes procyonoides*, 4 kg) and red fox (*Vulpes vulpes schrencki*, 4–5 kg). The lack of other large seed dispersers might increase the uniqueness and importance of brown bears as seed dispersers in Hokkaido. Their main diet in autumn is fresh fruits and acorns (Sato et al. 2004, 2005; Ohdachi et al. 2009; Shirane et al. 2021). The annual home ranges are 13.4–43.0 km^2 for the female bear and 199–462 km^2 for the male (Ohdachi et al. 2009). Bears are widely distributed around the island (77.8% of the island; Ministry of the Environment, Government of Japan 2019), although some local populations are still threatened (Ministry of the Environment, Government of Japan 2020). Thus, brown bears in Hokkaido may play a unique and vital role as seed dispersers.

In Hokkaido, human–bear conflicts, such as human injury and agricultural crop damage, have become severe social problems, probably due to population recovery and changes in anthropogenic land use (Sato 2017; Mano et al. 2020; Takinami et al. 2021). Thus, for the population management of brown bears in Hokkaido, reducing human–bear conflict is essential, as is the conservation of bears and their ecological functions, such as nutrient cycles (Koshino et al. 2013) and seed dispersal.

The objective of the present study was to evaluate the process of seed dispersal, from fruit consumption to germination, in brown bears in Hokkaido. To this end, we investigated: 1) gut passage time and the effect of gut passage on seeds through feeding experiments using captive bears, 2) seed dispersal distance using global positioning system (GPS) data for wild bears, and 3) the effects of gut passage and pulp removal on the germination rate of seeds.

Materials and methods

Feeding experiment

The feeding experiment was conducted from September to October 2021 using one male (age: 10 years and body weight: 237 kg) and one female (age: 13 years and body weight: 128 kg) housed at the Sapporo Maruyama Zoo (Sapporo, Japan). We selected three fleshy-fruited trees as the target plants: *Padus grayana* [(Maxim.) C.K. Schneid. (Rosaceae)], *Vitis coignetiae* [Pulliat ex Planch. (Vitaceae)], and *Actinidia arguta* [(Siebold et Zucc.) Planch. ex Miq. (Actinidiaceae)]. The fruits of these trees are some of the fruits most consumed by brown bears in Hokkaido (Sato et al. 2004, 2005; Shirane et al. 2021). The fruit of *P. grayana* contains one endocarp, which is considered the seed in this study. On average, the fruits of *V. coignetiae* and *A. arguta* contain 2.27 and 56.8 seeds per fruit, respectively (Y. Tsunamoto, personal observation). The longer diameter of the fruit and seed are 7.0 mm and 6.7 mm, 11.3 mm and 4.8 mm, and 19.0 mm and 2.3 mm, for *P. grayana*, *V. coignetiae*, and *A. arguta*, respectively (Masaki et al. 2012).

The bears were fed ripe fruits of the three species together (*P. grayana*: $n = 200$ fruits; *V. coignetiae*: $n = 200$ fruits; and *A. arguta*: $n = 38$–56 fruits) before regular feeding in the morning. The bears ate almost all the fruits within a few minutes. The regular diet of bears consisted mainly of vegetables and fruits. The seeds of regularly fed fruits were easily distinguished from those of the target fruits. No acclimation period was set because the number of target fruits fed was small compared with regular feeding. After feeding, the bears were released from a small indoor cage into an outdoor display space. The number of uneaten fruits was counted. The scats were sampled three times per day. Defecation time was recorded using video cameras (SMJP-W8410; SMONET Shenzhen, China). In the evening, the cameras were automatically switched to infrared mode. The first trial was conducted over 3 days. However, no seeds were detected on the second or third days. Subsequent trials were conducted until regular feeding was achieved on the following morning. The collected scats were washed with running water using sieves (mesh sizes: 4.0 mm, 1.68 mm, 1.2 mm, and 0.125 mm). Seeds were counted and categorized as intact seeds without pulp, broken seeds without pulp, and seeds with pulp. Two trials were conducted with each bear.

Germination test

From October to December 2021, the following four types of intact seeds of the three target species were sown in flowerpots (length: 55 cm, width: 15 cm, and height:15 cm) filled with culture soil: ingested seeds without pulp, ingested seeds with pulp, noningested seeds without pulp (manually washed seeds), and noningested seeds with pulp (intact whole fruit; Online Resource 1). The flowerpots were left outdoors in Sapporo, Hokkaido, Japan. The annual mean temperature, precipitation, and maximum snow depth at Sapporo in 2022 are 10.2 °C, 1154 mm, and 133 cm, respectively (Japan Meteorological Agency 2023). The soil was watered only when dry. During winter (December–March), the flowerpots were covered with snow. From April to August 2022, emerged seedlings were counted approximately twice a month. Weeds and seedlings were removed from pots to avoid competition.

Movement data and seed shadow estimation

GPS tracking was conducted on the Oshima Peninsula in southwestern Hokkaido, Japan, in 2009 and 2010. The original purpose of the tracking was to understand habitat use and the mechanisms of bear damage to agriculture. Bear habitats are a mixture of natural and plantation forests; natural forests are cool-temperate deciduous broad-leaved forests dominated by *Quercus crispula*, *Castanea crenata*, and *Fagus crenata*, whereas the main trees in the plantation forests are *Larix kaempferi*, *Abies sachalinensis*, and *Chryptomeria japonica*. These are the typical habitats of brown bears in Hokkaido. In 2009, GPS collars with a dropoff system using a countdown timer (GPS4400M, Lotek Wireless Inc., Canada) were attached to one subadult male (male-1; body weight: 66 kg) and two adult females (female-1; body weight: 103 kg and female-2; body weight: 108 kg). In 2010, GPS collars were reattached to female-2. The GPS loggers recorded locations on an hourly basis. The loggers recovered either after dropping off or when the bears were recaptured. Location data were collected only from August to November, which is the fruiting season for the target plants. The bear movement distance distribution during N hours (where, N is an integer from 1 to 24) is defined as the straight geographic distance between each recorded point and point N hours later. If the start or endpoint data were not validated or were missing, they were excluded from the analysis. To estimate the distribution of seed dispersal distance, a simulation of 10,000 seeds was conducted for each plant and bear. The distribution of GPT of the simulated seeds was set to the same proportion as that of the GPT obtained in the feeding trials for each target plant. The GPT of the male captive bear was used for male-1 and that of the female was used for female-1 and female-2. Subsequently, when the GPT of a seed was between $N-1$ and N hours, the dispersal distance of the seed was randomly selected from the distribution of the movement distance over N hours. For *A. arguta*, seeds without pulp and seeds with pulp were analyzed separately because many were defecated with pulp. Simulations and statistical analyses were performed using R software version 4.2.1 (R Core Team 2022). Source codes using these simulations is shown in Online Resources 2.

Results

Gut passage time

The proportion of recovered seeds ranged from 56.2% to 83.2% (Table 1). Most of the recovered seeds remained intact (Fig. 1A–C). Less than 6% of the seeds were classified as broken in all the trials and plants (Table 1). The proportion of seeds with pulp was low for *P. grayana* (0–1.6%) and *V. coignetiae* (0.5–12.4%), whereas for *A. arguta*, it varied depending on the trials and ranged from 1.1% to 47.5% (Table 1, Fig. 1D). The average GPT of intact seeds without pulp ranged from 3 h and 56 min to 6 h and 29 min (Table 1). A significant difference in GPT between seeds with and without pulp was detected for only three trials of *A. arguta* (those conducted from 20 to 21 September, 30 September to 1 October, and 12 to 13 October, 2021; $P<0.001$, t test with Bonferroni correction). In these trials, the average GPT of seeds with pulp was longer than those without pulp at 1:36, 2:39, and 3:01.

Germination

The germination rates of the defecated seeds without pulp were 32%, 51%, and 19% for *P. grayana*, *V. coignetiae*, and *A. arguta*, respectively (Fig. 2). The germination rate of seeds without pulp was significantly higher than that of seeds with pulp for *P. grayana* (noningested: $\chi^2=15.07$, df = 1, $P<0.001$; ingested: no germination of seeds with pulp) and *A. arguta* (noningested: $\chi^2=35.61$, df = 1, $P<0.001$; ingested: $\chi^2=26.14$, df = 1, $P<0.001$). In contrast, for *V. coignetiae*, the germination rate of seeds without pulp was significantly lower than that of seeds with pulp, depending on the treatment (noningested: $\chi^2=93.25$, df = 1, $P<0.001$; ingested: $\chi^2=0.1620$, df = 1, $P=0.687$).

Seed dispersal distance

The number of GPS points and positioning rates used were 1027 (49%), 328 (47%), 996 (42%), and 1542 (56%) for male-1, female-1, female-2 in 2009, and female-2 in 2010, respectively. Movement distance (average ± SD) over 5 h, which was almost equal to the average GPT for all the trials together, was 304 ± 351 m for male-1, 203 ± 266 m for female-1, 345 ± 430 m for female-2 in 2009, and 307 ± 476 m for female-2 in 2010 (Fig. 3). In

Table 1 Condition of seeds defecated by brown bear in Hokkaido and their gut passage time (GPT); GPT is shown as average ± standard deviation

Padus grayana

Experiment period	Sex	Total: Number of seeds	Total: GPT	Intact seeds without pulp: Number of seeds	Intact seeds without pulp: GPT	Broken seeds without pulp: Number of seeds	Broken seeds without pulp: GPT	Seeds with pulp: Number of seeds	Seeds with pulp: GPT
7–9 September	Female	165 (82.5%)	4:53 ± 0:46	152 (76.0%)	4:54 ± 0:46	11 (5.5%)	4:52 ± 0:44	2 (1.0%)	3:43 ± 0:00
30 September–1 October	Female	149 (81.4%)	5:56 ± 1:58	140 (76.5%)	5:55 ± 2:14	6 (3.3%)	6:43: ± 1:52	3 (1.6%)	5:07 ± 0:53
20–21 September	Male	77 (56.2%)	4:32 ± 0:59	71 (51.8%)	4:32 ± 1:01	6 (4.4%)	4:18 ± 0:55	0 (0.0%)	
12–13 October	Male	156 (78.0%)	5:35 ± 1:45	154 (77.0%)	5:35 ± 1:45	2 (1.0%)	4:59 ± 1:08	0 (0.0%)	

Vitis coignetiae

Experiment period	Sex	Total: Number of seeds	Total: GPT	Intact seeds without pulp: Number of seeds	Intact seeds without pulp: GPT	Broken seeds without pulp: Number of seeds	Broken seeds without pulp: GPT	Seeds with pulp: Number of seeds	Seeds with pulp: GPT
7–9 September	Female	316 (75.3%)	4:27 ± 0:47	264 (62.9%)	4:20 ± 0:47	0 (0.0%)		52 (12.4%)	5:02 ± 0:50
30 September–30 October	Female	330 (72.7%)	6:29 ± 1:56	285 (62.8%)	6:29 ± 1:56	1 (0.2%)	05:37	44 (9.7%)	6:32 ± 1:59
20–21 September	Male	312 (83.2%)	5:01 ± 1:01	310 (82.7%)	4:59 ± 1:01	0 (0.0%)		2 (0.5%)	5:29 ± 0:00
12–13 October	Male	283 (63.0%)	6:13 ± 0:53	274 (61.0%)	6:13 ± 0:54	0 (0.0%)		9 (2.0%)	6:29 ± 0:12

Actinidia arguta

Experiment period	Sex	Total: Number of seeds	Total: GPT	Intact seeds without pulp: Number of seeds	Intact seeds without pulp: GPT	Broken seeds without pulp: Number of seeds	Broken seeds without pulp: GPT	Seeds with pulp: Number of seeds	Seeds with pulp: GPT
7–9 September	Female	1894 (59.5%)	3:56 ± 0:32	1857 (58.4%)	3:56 ± 0:33	1 (0.0%)	03:43	36 (1.1%)	3:43 ± 0:00
30 Seprember–1 October	Female	1609 (69.1%)	6:05 ± 1:25	1243 (53.4%)	5:24 ± 1:29	1 (0.0%)	05:37	365 (15.7%)	8:25 ± 4:40
20–21 September	Male	1769 (82.0%)	4:45 ± 1:02	1127 (52.2%)	4:12 ± 0:49	15 (0.7%)	4:59 ± 0:59	627 (29.1%)	5:44 ± 1:10
12–13 October	Male	1963 (75.2%)	6:36 ± 2:16	723 (27.7%)	4:56 ± 1:38	0 (0.0%)		1240 (47.5%)	7:35 ± 3:32

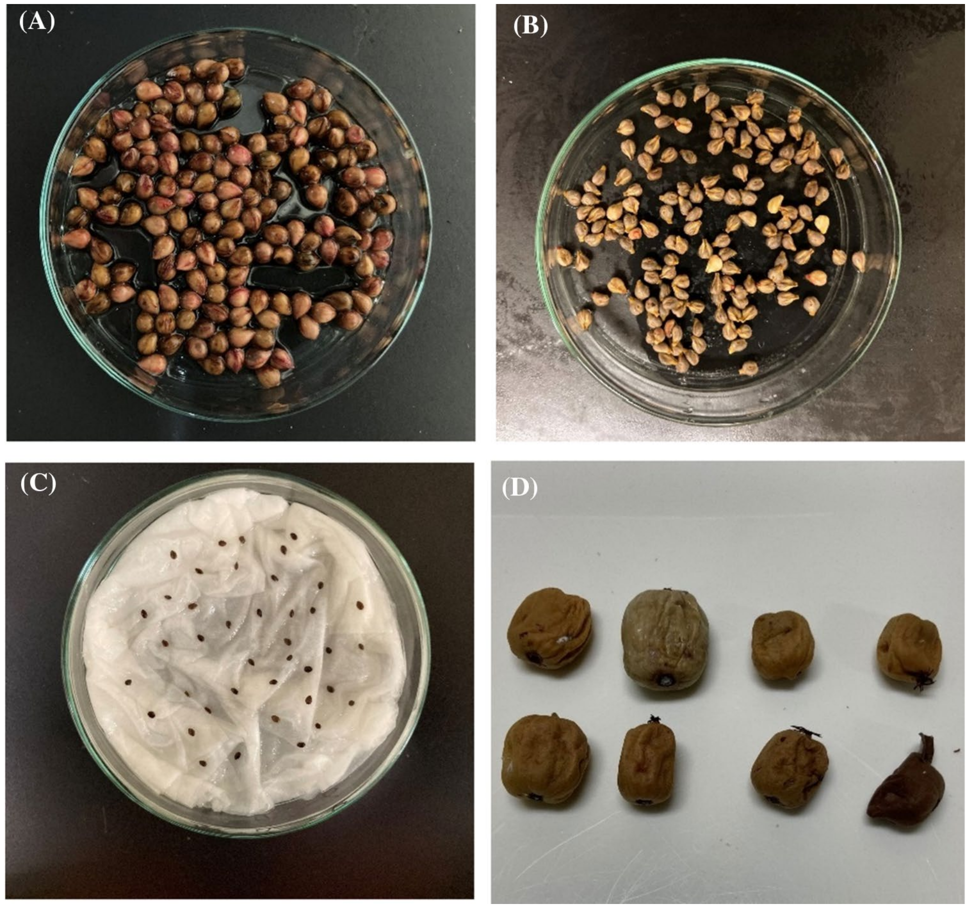

Fig. 1 Seeds of **A** *P. grayana*, **B** *V. coignetiae*, **C** *A. arguta* (without pulp), and **D** *A. arguta* (with pulp), collected from the feces of a captive brown bear (*Ursus arctos*)

2009, there were significant differences in the movement distance between bears throughout 18 h (maximum GPT; $P < 0.001$, Wilcoxon rank-sum test with Bonferroni correction; Online Resource 3). In contrast, there was no significant difference in the movement distance between female-1 and female-2 throughout 2 and 5 h, and between male-1 and female-2 throughout 5 h ($P > 0.05$, Online Resource 3). Compared with 2010, the movement distance for female-2 in 2009 throughout 18 h was significantly longer ($P < 0.001$), but no significant difference in movement distance was detected between the durations of 2 h and 5 h ($P > 0.5$; Online Resource 3).

The average and median seed dispersal distances for each bear and plant ranged from 181 to 345 m and 62 to 202 m, respectively (Fig. 4). Significant differences in distance distribution were detected for some combinations of plants (e.g., female-1: *P. grayana* versus *A. arguta*), individual bears (e.g., *P. grayana*: male-1 versus female-2), and years (e.g., *P. grayana*: female-2 in 2009 versus female-2 in 2010; Kolmogorov–Smirnov test with Bonferroni correction, $P < 0.001$, Online Resource 4). For *A. arguta*, the dispersal distance of seeds with pulp was significantly longer than that of seeds without pulp for all individuals (Kolmogorov–Smirnov test, $P < 0.001$, Online Resource 5).

Discussion

Seeds of all three examined plant species were successfully dispersed and germinated after consumption by brown bears in Hokkaido, Japan. Therefore, brown bears are considered to be effective seed dispersers.

GPT and condition of defecated seeds

In the feeding experiments, 16.8–43.8% of the seeds were unrecovered. Some may have been completely crushed during the digestion. Others were probably missed during fecal collection or washing. Therefore, the proportion of intact seeds was underestimated in this study. However, over 50% of the seeds were defecated intact in all trials and species, suggesting that bears were seed dispersers rather than seed predators of the three target plants.

The average GPT of brown bears ranged from 3 h and 43 min to 8 h and 25 min (Table 1), which is similar to that of brown bears from North America (7 h, Pritchard et al. 1990) and Scandinavia (6 h, Elfström et al. 2013). The average GPT for the brown bear is also similar to that for the Asiatic black bear (*Ursusu thibetanus*, 5.1–6.1 h on average; Koike et al. 2011) and for the American black

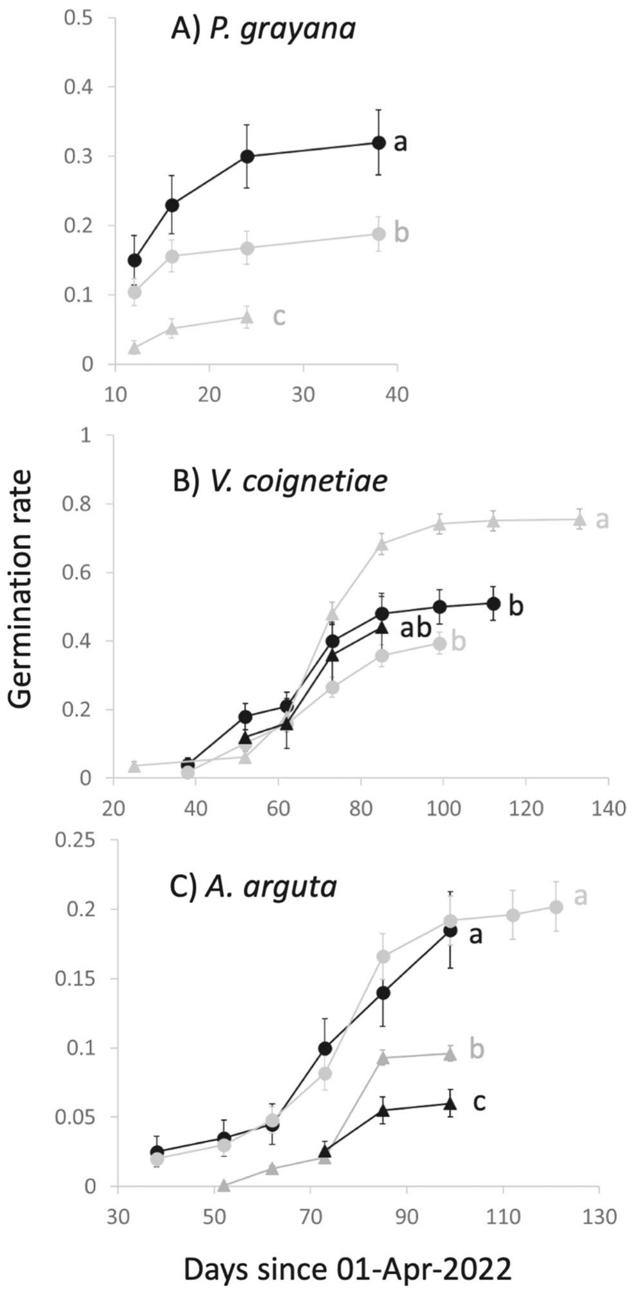

Fig. 2 Rate and timing of germination for ingested (without pulp, black circles), uningested (without pulp, grey circles), ingested (with pulp, black triangles), uningested (with pulp, grey triangles). Error bars represent standard error. Different lowercase letters indicate significant differences between curves detected by the log-rank test (with Bonferroni corrected P value < 0.05)

bear (*Ursus americanus*, 6.9 ± 0.6 h; Pritchard and Robbins 1990). However, the maximum GPT of the Asiatic black bear, which has a smaller body size, was more than 40 h, more than two times longer than that of the brown bear in our study. This difference can probably be attributed to the digestive process of Asiatic black bears, which are more attuned to plant diets.

Pritchard and Robbins (1990) and Elfström et al. (2013) reported that the GPT of captive brown bears increased to 13–14 h when the main diet was changed from plant to animal material, which is poor in dietary fiber. In our study, the main diet of captive and GPS-tracked bears was plant material, which confirmed our results. However, the diets of brown bears are highly flexible and depend on local and seasonal food availability (Haroldson et al. 2020; Swenson et al. 2020). Before the modernisation of Hokkaido (ca. 100–200 years ago), brown bears in Hokkaido were likely more dependent on animal materials (Matsubayashi et al. 2015). Moreover, in eastern Hokkaido, brown bears often consume animal materials such as salmonid fish (Shirane et al. 2021) and sika deer (*Cervus nippon*, Kobayashi et al. 2012). In such cases, brown bears in Hokkaido are likely to contribute to long-distance dispersal even if the dispersal quantity decreases.

Wild bears often consume large amounts of fruits (Shakeri et al. 2018; García-Rodríguez et al. 2021a), especially during hyperphagia (excessive eating before hibernation in winter). GPT may be affected by eating large quantities of food and physiological changes during hyperphagia. However, in our feeding trials, captive bears were kept without hibernation, and the target fruits fed on (< 200 fruits) accounted for only a small proportion of the diet. Furthermore, number of trials were only four. To understand GPT in the wild, factors affecting GPT, and the condition of defecated seeds, direct measurement of GPT in the wild (Beirne et al. 2019) or feeding experiments under various conditions should be conducted in the future.

Seed dispersal distance

The mean and median seed dispersal distances for brown bears ranged from 181 to 345 m and 62 to 176 m, respectively (Fig. 4, Online Resource 4). Compared with other mammalian seed dispersers in Japan, the maximum dispersal distance for the brown bear is approximately the same as that of the Asian black bear (Koike et al. 2011, 2022) and the Japanese marten (*Martes melampus*, Tsuji et al. 2016; Koike et al. 2022) but longer than that of the Japanese macaques (*Macaca fuscata*, Terakawa et al. 2009; Tsuji and Morimoto 2016; Koike et al. 2022), badger (*Meles anakuma*, Tsunamoto et al. 2020b; Koike et al. 2022), and raccoon dog (*Nyctereutes procyonoides*, Tsunamoto et al. 2020b; Koike et al. 2022). Although brown bears contributed to long-distance dispersal, the frequency peaks occurred at short distances, resulting in small median values (65–202 m; Fig. 4).

The movement patterns of bears change depending on the landscape structure and/or distribution of food resources. The acorn crop size under the fruiting trees in the study area was smaller in 2009 than in 2010 (*C. crenata* 28.4 fruits/m^2 in 2009, 55.8 fruits/m^2 in 2010; *Q crispula* 3.1 fruits/m^2

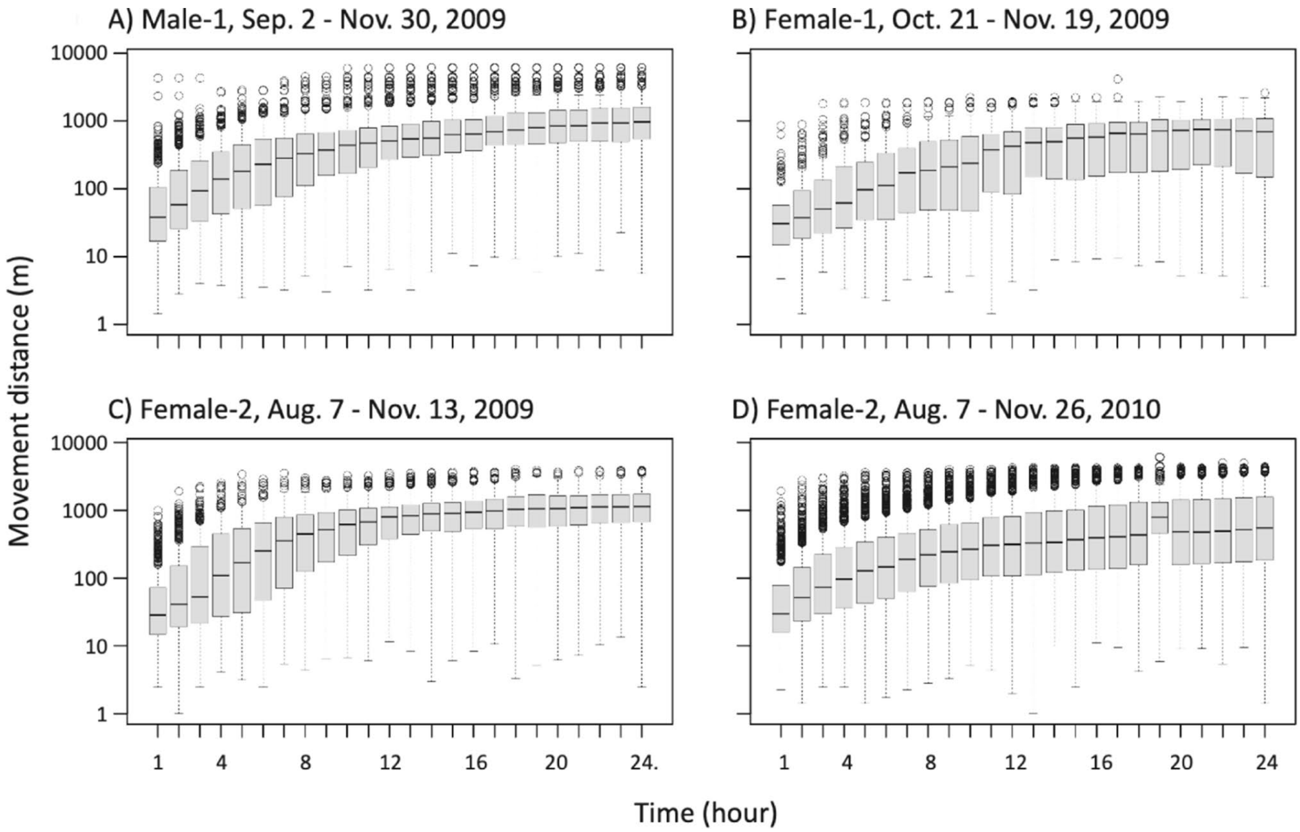

Fig. 3 Movement distance of three wild brown bears in Hokkaido

in 2009, 35.8 fruits/m^2 in 2010; H. Tsuruga, unpublished data). The movement distance of brown bears over 18 h was greater in 2009, probably because of the search for scarce food resources (Fig. 3, Online Resource 3). This is consistent with the finding that the use of farmland by brown bears increases during years of low acorn production (Sato and Endo 2006). Furthermore, reflecting the longer movement distance, seed dispersal distance was longer in 2009 for all three target plants (Fig. 4; Online Resource 4). However, in this study, only one individual bear was tracked for 2 years. To understand the general pattern of among-year variation, we should track more bears over multiple years. Brown bears are widely distributed around Hokkaido and inhabit various habitats, including coastal sand dunes, peat bogs, shrublands, farmlands, and forests (Ohdachi et al. 2009). As a result, the home range of the brown bear in Hokkaido also varies among regions (e.g., 13.4 km^2 in Shiretoko and 43.0 km^2 in Urahoro; Ohdachi et al. 2009). Moreover, even for the same location and year, differences in dispersal distances were detected between individual bears and plants (Fig. 4, Online Resource 4). These results suggest that seed dispersal distance for brown bears is context-dependent and is affected by complex factors such as sex, body size, season, and plant traits. Although our findings that brown bears are effective seed dispersers are robust, data from various plant species and sites are required to understand the effects of these factors.

Germination

The pulp of fleshy fruits often inhibits germination due to chemical inhibition and the physical condition of the pulp (Traveset et al. 2007). This is consistent with our finding that pulp had a negative effect on the germination of *P. grayana* and *A. arguta* (Fig. 2A, C). However, for *V. coignetiae*, the pulp had no significant effect on the ingested seeds but had a positive effect on uningested seeds (Fig. 2B). Previous studies on brown bears have reported that the effects of depulping (via digestion in brown bears) on germination are positive, negative, or insignificant, depending on the plant (Applegate et al. 1979; Traveset and Willson 1997; Steyaert et al. 2019; García-Rodríguez et al. 2021b). However, even if the germination rate was low, the defecated seeds of all plants studied could germinate, suggesting that the regeneration of seeds after bear digestion is possible.

Seeds of intact fruits germinate when buried in the soil. Yagihashi et al. (2000) reported that the whole intact fruits of two cherry species did not germinate when incubated

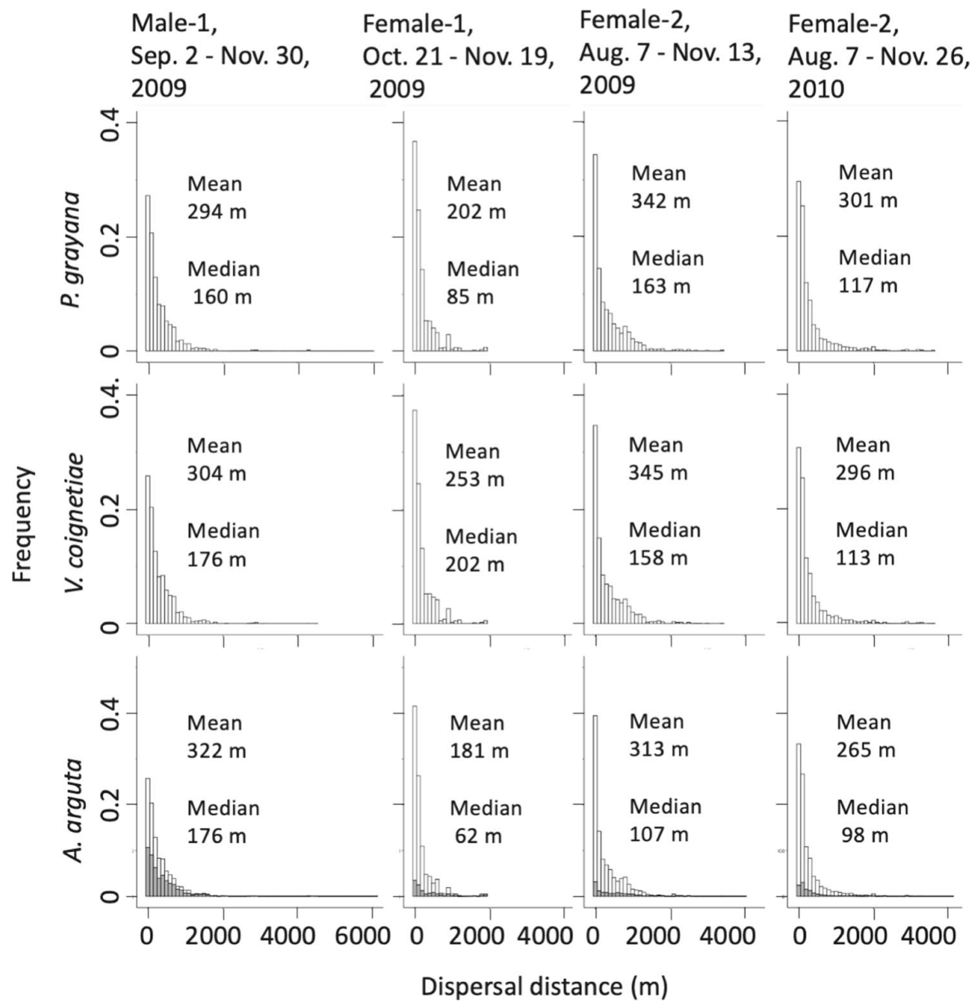

Fig. 4 Distribution of estimated seed dispersal distance by brown bear. For *A. arguta*, grey and white bars represent seeds with and without pulp, respectively. For *P. grayana* and *V. coignetiae*, dark grey bars represent both types of seeds

in Petri dishes under sterile conditions. Furthermore, *A. arguta* seeds do not germinate under the same conditions (Y. Tsunamoto, unpublished data). In our study, the pulp likely decomposed during winter in outdoor soil conditions. These results indicate that animal dispersal may not be necessary for plant regeneration.

For the germination test, seeds and seedlings were maintained at a low density in a suitable environment. However, seeds are often dispersed in the wild at high density in unsuitable sites (e.g., lack of light or moisture). Therefore, even if the germination rate is high under controlled conditions, most seeds do not survive in the wild because of illness, predation, or competition. Secondary dispersal by rodents (Shakeri et al. 2018; Levi et al. 2020), dung beetles (Koike et al. 2012), or abiotic factors such as rain and wind may be essential to increase the survival rate. Tracking the fate of dispersed seeds in the wild is challenging, but it is crucial to fully understand the seed-dispersal function of brown bears.

Effects of pulp

The proportion of seeds with pulp varied considerably among the species (Table 1). In particular, in some trials of *A. arguta*, a large proportion of seeds had pulp (maximum 63% for the trial from 12 to 13 October). In the feeding trials, the level of fruit maturation was not constant, although the fruits were sufficiently ripe for germination. The fruit was likely defecated intact when the pulp was hard because of the early stage of fruit maturation. The GPT of seeds with pulp was significantly longer than those without pulp (Table 1). In Japanese macaques, the GPT of heavier seeds is longer than lighter seeds (Tsuji et al. 2010). Similarly, the movement of intact fruits may be restricted during digestion because of their large size. In *A. arguta*, the germination rate of the defecated seeds with pulp was lower than that of the seeds without pulp (Fig. 2). To the best of our knowledge, this is the first study to report that fruit pulp inhibits germination even after gut passage. The dispersal distance of *A. arguta* seeds with pulp was greater than that of seeds without pulp (Fig. 4, Online Resource 5), which could be attributed to long GPT. Seeds of wild bear scats often retain their pulp, which is sometimes similar to that of an intact fruit (Y. Tsunamoto, personal observation). These seeds may contribute substantially to gene flow or range shifts despite low germination rates.

Function of the brown bear in Hokkaido as a seed disperser

One advantage of seed dispersal by brown bears is the movement of seeds away from the mother plant. A large maximum dispersal distance contributes to gene flow between distant habitats. Long-distance dispersers are vital for rapid migration in response to shifts in suitable habitats for plants caused by climate change (Corlett and Westcott 2013; Lenoir and Svenning 2015). In addition to the qualitative components of dispersal effectiveness, such as dispersal distance or microhabitat of the deposition sites, the number of seeds dispersed by bears is often remarkably high (Shakeri et al. 2018; Tsunamoto et al. 2020a; García-Rodríguez et al. 2021a, b). However, the effects of gut passage on germination are not always positive and depend on the plant species.

The target plants in this study are also common in isolated forests or small neighbouring islands, which brown bears do not inhabit. This suggests that plant regeneration does not always require seed dispersal by brown bears. In these areas, animals such as the red fox (*Vulpes vulpes schrencki*, Tsukada and Nonaka 1996), raccoon dogs (Koike and Masaki 2019), the Japanese sable (*Martes zibellina brachyura*, Murakami 2003), the Japanese marten (Koike and Masaki 2019), and frugivorous birds (Yoshikawa et al. 2009) contribute to seed dispersal. However, seed dispersal by other animals or natural fall from trees results in a short dispersal distance. Strong spatial aggregation (Harrison et al. 2013; Caughlin et al. 2015) and genetic structures (Collevatti et al. 2003) occur in such scenarios, resulting in long-term changes in plant population dynamics.

The present study found that brown bears in Hokkaido play an important ecological role as seed dispersers. Thus, in managing brown bears in Hokkaido, such ecological functions should be considered, apart from conserving the bear population itself and reducing human–bear conflicts.

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Author contributions Y.T. conceptualized the study and conducted feeding trials, germination experiments, and data analysis. H.T. conducted GPS tracking of wild bears. K.K., T.S., and T.A. conducted the feeding trials. Y.T. drafted the original manuscript. All the authors contributed to the review and editing of the manuscript.

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Data availability The datasets used and(or) analyzed in the current study are available from the corresponding author upon reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest Not applicable.

Ethics approval All animal experiments were conducted according to standards relating to the Care and Keeping and Reducing Pain of Laboratory Animals (Notice of the Ministry of the Environment, Government of Japan, no. 84 of 2013).

Consent to participate Not applicable.

Consent for publication Not applicable.

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