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ORIGINAL ARTICLE

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Fruit phenology of *Prunus jamasakura* and the feeding habit of the Asiatic black bear as a seed disperser

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Abstract We investigated the relationship between the fruit phenology of *Prunus jamasakura* and the fruit-feeding period of the Asiatic black bear (*Ursus thibetanus*). The purposes of this study were to determine (1) when bears feed on the fruit of *P. jamasakura* in relation to phenology; (2) whether ingestion damages seeds; and (3) how ingestion influences seed germination. We assessed the relationship between the phenology of fruit maturation (size, sugar concentration, color, persistence, and germination percentage) and the feeding period of bears in the field, as judged from bear shelves and claw marks. We also compared the germination percentage of seeds ingested by captive bears with that of uningested. Bears fed on the fruit from days 50 to 66 after flowering, when most of the fruits were on the tree and became large, the germination percentage of seeds increased, and the sugar concentration became high. Bears fed only on mature fruits and so obtained high-quality nutrients. Germination tests showed that ingestion of fruits by the bears caused no physical damage to the seeds. Ingested seeds did not show a significant difference in germination percentage from seeds, whose pulp was artificially removed. These results indicate that bears are potentially effective dispersers from a qualitative perspective and, to some extent, from a quantitative perspective.

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Introduction

In general, most fleshy fruits are adapted for consumption by various vertebrates, and seeds within them presumably rely on vertebrates for dispersal (Howe 1986; Willson 1993). Several studies have indicated that primates as well as birds and bats and, recently, some carnivores act as seed dispersers (Herrera 1989; Hickey et al. 1999; Otani 2002).

Seed dispersal by bears is reported in studies of the Asiatic black bear (*Ursus thibetanus*) (Koike et al. 2003; Sathyakumar and Viswanath 2003), American black bear (*U. americanus*) (Rogers and Applegate 1983; Janen et al. 2002), brown bear (*U. arctos*) (Applegate et al. 1979; Willson and Gende 2004), sun bear (*Helarctos malayanus*) (McConkey and Galetti 1999), and sloth bear (*Melursus ursinus*) (Sreekumar and Balakrishnan 2002). Many of these studies have focused on the germinability of ingested seeds in feces. The Asiatic black bear is one of the largest mammals that inhabit Honshu and Shikoku, Japan. The Asiatic black bear has sectorial or bunodont cheek teeth, which minimize damage to seeds (Koike et al. 2003) and has a large home range (Hazumi 1998: ca. 26.4–66.1 km^2). From these features and gut retention time (Traveset and Willson 1997), bears are expected to be an effective seed disperser (Willson 1993). However, previous germination tests of ingested seed from feces were insufficient to evaluate the efficiency of bears as seed dispersers because they can't provide the information what is the effect of the vertebrate gut on germination (Applegate et al. 1979; Rogers and Applegate 1983; Samuels and Levey 2005). To determine whether bears play an important role as agents of seed dispersal, it is necessary to take the following two points into consideration.

First, it is important to consider the feeding period in terms of seasonal fruiting phenology. Asiatic black bears mostly climb trees to feed on fruits before the fruits drop to the ground (Bromley 1965). If fruits are ingested after seed maturation, dispersed seeds could germinate. Therefore, whether bears are effective seed dispersers can be judged by examining the relationship between the fruit-feeding period of bears and the phenology of fruits and seed maturation.

Second, the effect of bear defecation on seed germination is not yet understood. Previous studies on some plant species were revealed that the ratio of germination that pass through the gut in apparently good condition differed from the ratio of those that do not (e.g., Rogers and Applegate 1983). Bird ingestion can enhance germination by pulp removal and by modification of the seed coat structure (Agami and Wisel 1986; Yagihashi et al. 1999; Samuels and Levey 2005). These studies, however, did not sample the seeds throughout the maturation processes. The effect on seed germination might change depending on the fruit phenology. Therefore, the effect of ingestion needs to be tested using fruits over the whole maturation period.

For three reasons, we chose the fruit of *Prunus jamasakura* to answer the three questions posed below. First, *P. jamasakura* is a common species in the deciduous forest in central Japan (Oba 1989) and its seeds are frequently found in fecal samples of the Asiatic black bear (Koike et al. 2003). Second, *P. jamasakura* is one of the rare woody species bearing fleshy fruits during June–July (Koike unpublished) and, therefore is likely a common food item of Asiatic black bears in that period. Third, the *Prunus* fruit is a typical drupe, and the procedure to test germination of *P. jamasakura* seed is well established (Ishii 1991).

This study assessed the following points: (1) When do the bears feed on *P. jamasakura* fruit in relation to phenology? (2) Are broken or cracked seeds of this species defecated by bears? (3) How does ingestion by bears affect the seed germination during the maturation of fruits? On the basis of the results, we discuss the significance of the Asiatic black bear is as a seed disperser of *P. jamasakura*.

Methods

Study sites

Field studies were conducted at Ashigawa village located in the northern part of Mt. Fuji. The area is mountainous, and range from 600 to 1,650 m in elevation. The mean temperature of the year is 6–8°C and the annual precipitation is 1,800–2,000 mm (Yamanashi Prefecture 1997). Ashigawa area is consisted of secondary forests dominated by *Fagus crenata*, *Quercus crispula*, *Q. serrata*, and *Castanea crenata* (Miyawaki et al. 1977), and the fruit of *P. jamasakura* ripens from late June to early August. We investigated the fruit phenology of *P. jamasakura* and the pattern of feeding on *P. jamasakura* by bears at the two study sites (foothill site (elevation 600–750 m) and mountain site (elevation 750–1,150 m, Table 1)). Bears are found only at the mountain site. The major frugivores of *P. jamasakura* fruit are birds and carnivores such as bears or marten (*Martes melampus*) at the mountain site and birds at the foothill site.

Table 1 Details of sites for study of fruit phenology of *Prunus jamasakura* and the feeding period of Asiatic black bear and number of sample trees

Site	Elevation (m)	Bear presence	Study object
Mountain	750–1,150[a]	Yes	Flowering date (n = 102) Bear feeding date (n = 102)
Foothill	600–750[a]	No	Flowering date (n = 3) Fruit phenology of *Prunus jamasakura* (n = 3)

[a] Yamanashi Prefecture (1997)

Study design

We investigated the feeding pattern of bears on *P. jamasakura* fruits throughout the fruit maturation period. At the mountain site, where the bears live, there were no suitable trees for observing the detailed fruiting phenology, because the *P. jamasakura* trees form part of the high tree layer in the forest. Fortunately, the *P. jamasakura* fruit maturation period can be calculated from the flowering day (Ishii 1991). Therefore, we used the results of the fruit phenology at the foothill site, where bears do not live and the bear feeding period data at the mountain site.

To clarify the phenology of *P. jamasakura* fruits, we ascertained the flowering date of three *P. jamasakura* trees and regularly monitored the fruit phenology. At the same time, the flowering date of the 102 *P. jamasakura* trees were only determined by a method mentioned later at the mountain site where the bears inhabits. The condition of *P. jamasakura* fruits on which bears had fed was calculated from the calendarial dates when bears fed, the number of passing days after the flowering date of the tree from which bears fed, and the phenology results of *P. jamasakura* fruits at the foothill site.

The phenological details recorded were fruit color, the number of fruits persisting, the form of lost fruit (with or without pedicel, as an indicator of physiological fruit drop or of predation by birds, respectively), the size of fruits, the size of seeds, seed maturation, and the sugar concentration. We carried out these investigations except for sugar concentration from 1 April to 31 July 2001. Sugar concentration was measured from 1 April to 31 July 2005.

Decision on flowering date

At the foothill site, we chose three *P. jamasakura* trees (DBH > 20 cm) to monitor flowering day every day in

April 2001. At the mountain site, we established survey routes (total of 24.1 km; 750–1,100 m in elevation), and chose 102 *P. jamasakura* trees (DBH > 20 cm) (44 trees 750–850 m; 38 trees 850–950 m; and 20 trees 950–1,050 m) along the route to monitor flowering date every day from April to May 2001.

We sampled ten branches at random from each sample tree and counted the flowering buds on each branch within the range of 50 cm length and 20 cm width (10 cm each side of the branch) from the tip of the branch. The flowering ratio was defined as the number of flowering buds divided by the total number of buds. When the average flowering ratio reached 80%, that day was defined as the ''date of flowering'' for each tree.

The ''day *n*'' in the following text represents the date *n* days after the flowering date.

Fruit color and persistence

We selected 200 fruits from each tree and tagged every pedicel on day 22 at the foothill site. The fruit color and the number of persisting pedicels were visually checked every 2 days from days 22 to 74. All fruit was green before day 20. The fruit color was defined as green when the exocarp was all green; red-green when the exocarp had a small red part; red when the red portion exceeded 50% of the surface; and black when the black portion exceeded 50% of the exocarp.

If any of the sample fruits were missing, we searched on and around the tree to retrieve the tagged pedicels in order to determine how the fruit were removed. Fruit missing a pedicel was called ''fruit without pedicel''. Fruit retaining a pedicel was called ''fruit with pedicel''. When we observed the bird ingested the fruit during the survey, we recorded the feeding style of the fruits. We have observed that when birds feed on fruits of *P. jamasakura*, they leave the pedicels attached to the tree.

Fruit and seed size, and seed maturation

We randomly sampled 30 fruits per tree at the foothill site every 2 days from days 10 to 74, and measured the fruit and seed diameter. To examine the maturation of seeds, we washed off the exocarp and mesocarp with water, then conducted germination tests according to Ishii (1991). Germination was defined as when a root appeared and the embryo became as long as the seed itself.

Sugar concentration

We randomly sampled 15 fruits of each color per tree in the foothill site every 2 days from days 32 to 74, and analyzed the sugar concentration in the mesocarp using the gas–liquid chromatography (Shimadzu CA-4PJ) according to the method described by Sweeley et al. (1962). The period of examination is different though this examination used the same trees as other examinations.

Feeding date

We monitored the 102 trees in the foothill site every five days from days 10 to 45 and then daily after day 45 until they no longer bore fruit. Two criteria were used to judge, which fruits had been eaten: claw marks left on the stems and the presence of a ''bear shelf'' (a pile of broken branches in the treetops, formed by bears reaching for berries). During each survey, we recorded the claw marks, photographed the bear shelf, and removed broken branches and leaves on the ground to avoid duplicate counts. We carried out this survey from 1 April to 31 July 2001.

Germination test of ingested seeds

At the Institute of the Japanese Black Bear in Ani, we conducted germination tests of seeds that had passed through the gut of captive bears. We sampled *P. jamasakura* seed at five phenological stages (days 50, 55, 60, 65, and 70) in the Tokyo University of Agriculture and Technology in Fuchu, Tokyo, and carried out this test six times at each stage, using two adult bears with three times replications from 20 to 30 May 2002 and from 15 to 30 July 2004.

After 200 samples (100 green + 100 red [day 50 only] or black) of *P. jamasakura* fruit were fed to the bears within an hour, we collected all remaining fruit. We collected all feces and washed them with water through screens to sort out seeds (intact and damaged), and used them for the germination test (i.e., ingested seed). After ingestion, the seed was defecated in 5–37 h.

At the same time, we collected other fruits for two control treatments: seeds from which the exocarp and mesocarp were washed off (''exposed seeds'') and intact fruits with seeds within (''wrapped seeds''). The latter were naturally fallen fruits. Germination tests included six replications with 100 seeds in each treatment. These were done under the same conditions as the germination test mentioned before. After post-chilling incubation, the viability of the remaining ungerminated seeds was checked by the tetrazolium staining method or by cutting seeds to examine their albumen (McDonald and Copeland 1989).

The experimental procedures used in this study followed the Guidelines on Concerning Animal Experimentation by the Japanese Association for Laboratory Animal Science.

Results

Flowering date

The dates of flowering of sample trees were 13 April 2001 and 15 April 2005 at the foothill site. The dates of flowering of sample trees were between 13 April and 3 May 2001 at the mountain site. The date of flowering was delayed due to the higher altitude.

Fruit color and bearing number

Figure 1a shows the changes in proportion of fruits of different color. All samples were recorded as green until day 38. Red-green fruit then appeared on day 40, followed by red on day 46 and black on day 54. Red and black exceeded 50% on day 56, and 80% on day 62. In contrast, the ratio of green fruit decreased rapidly.

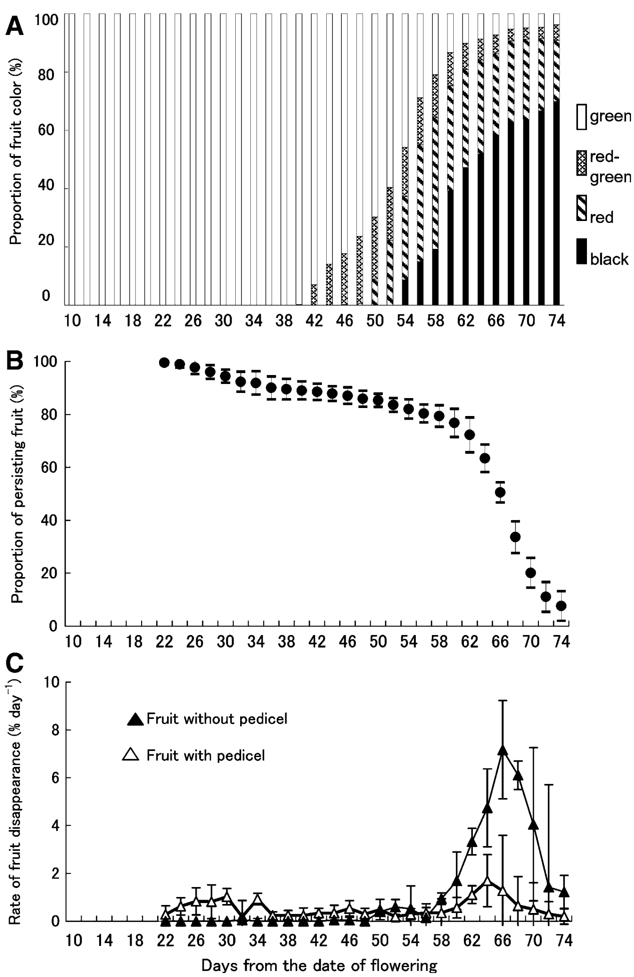

Fig. 1 Fruit phenology of *Prunus jamasakura* and disappearance pattern. **a** Change in color of fruits on trees. **b** Proportion of fruit that remained on trees (mean ± SD). **c** Rate of fruit disappearance per day (mean ± SD) after the date of flowering. *Open triangles* "fruit with pedicel", *closed triangles* "fruit without pedicel". $n = 200$

The proportion of persisting fruit decreased gradually until day 60 (Fig. 1b), then decreased rapidly by 64.7% in 10 days.

Figure 1c shows the rate of fruit disappearance by pedicel falling type. There was no clear change in the percentage of the "fruit with pedicel" type from days 22 to 74; the average rate of disappearance was $0.6 \pm 0.4\%$ day^{-1} (0.4–3.4%). All fruits of the "fruit with pedicel" type were discovered around the bases of the trees. On the other hand, the percentage of "fruit without pedicel" type increased from around day 62. The rate of fruit disappearance averaged $0.7 \pm 0.6\%$ day^{-1} (0.3–3.3%) from days 50 to 60, but $4.0 \pm 2.3\%$ day^{-1} (2.5–14.3%) from days 62 to 74.

Fruit size and seed size

Means of fruit size were not different among fruits of different colors (Kruskal-Wallis test, $df = 1$–3, $P = 0.11$–0.85). Fruit size increased from days 10 to 20, from days 34 to 36, and from days 50 to 58. No change in diameter was seen after day 58 (Fig. 2a). Fruit diameter increased in a double sigmoid growth curve and showed three phenological stages.

Seed size became measurable beyond day 28, when the endocarp hardened. There was no dear variation in diameter among fruit colors at the same stage (Kruskal-Wallis test, $df = 1$–3, $P = 0.07$–0.92). Seed size was almost constant at all stages (Fig. 2a).

Sugar concentration

Sugar concentration is not even among different-colored fruit (Kruskal-Wallis test, $df = 1$–3, $P < 0.01$). The sugar concentration increased as the fruit matured (Fig. 2a, b).

Seed maturation

No germination was observed until day 44 (Fig. 2c). The percentage rose rapidly on day 50 to $46.1 \pm 11.6\%$, and then gradually until day 66. Germination percentages were not different among fruit color (Kruskal-Wallis test, $df = 1$–3, $P = 0.35$–0.69).

Feeding date

We found 27 claw marks on 24 trees at the mountain site. Evidence of feeding on the fruits was observed from days 50 to 66 (Fig. 3). The evidence found on day 50 was only a claw mark, but all other cases featured bear shelves and scattered branches and leaves on the ground under the tree. The fact that 17 signs (63%) were recorded from days 58 to 62 showed intensive use during this period. Furthermore, three trees were visited twice

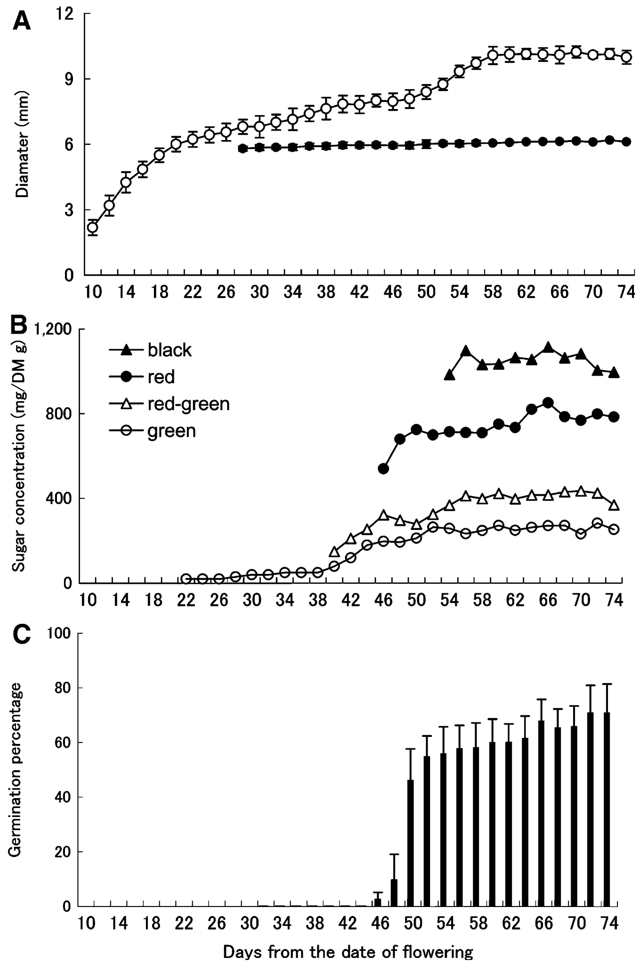

Fig. 2 Fruit phenology of *Prunus jamasakura*. **a** Changes in fruit diameter (mm; mean ± SD of all colors) and seed diameter (mm; mean ± SD of all colors) after the date of flowering. **b** Changes in sugar concentration (mg/g DM) of fruit of each color after the date of flowering. $n = 15$. **c** Rate of seed germination (mean ± SD of all colors) after the date of flowering. In **a** and **c**, $n = 30$ from days 10 to 74. Each survey sampled from each tree

by bears: one tree on days 58 and 64, one on days 59 and 64, and the third on days 55 and 58.

Based on the fact of bear signs, bears ate *P. jamasakura* fruit over 28 days, from 5 June to 2 July 2001 (Fig. 4). Bears visited *P. jamasakura* trees at altitude later ($n = 102$, $r^2 = 0.875$, $P < 0.001$; Fig. 4).

Effect of ingestion on germination

Bears ingested significantly more red (day 50 only) or black fruits (92–100%) than green fruits (4–7%) (binomial test $df = 5$, $P < 0.001$). The proportion of apparently intact seeds in feces exceeded 95% regardless of phenological stage (Table 2).

In the analysis of germination ratio, we used only black and red (day 50 only) fruits, because the number of green fruits ingested was small (Table 2). The final germination percentages of ingested seeds and exposed seeds ranged between 44 and 63%, and did not differ significantly among any phenological stages (binomial test $df = 5$, $P > 0.05$ for all stages). After the 60-day germination experiment, all the ungerminated ingested seeds and exposed seeds were found to be nonviable. In contrast, no wrapped seeds germinated during the germination test, although 54.5 ± 6.9% of them were viable (Table 3).

Discussion

Relationship between fruit phenology and the feeding period of bears

Our findings demonstrated that bears potentially function not as seed predators, but as seed dispersers, of *P. jamasakura*. It is obvious from the germination test that the percentage of *P. jamasakura* germination increased after day 50. The feeding signs showed that bears started to feed on *P. jamasakura* fruit on day 50, and fed especially during the period from days 58 to 62 (Fig. 3). Therefore, feeding on fruits of *P. jamasakura* occurred after seed maturation.

The bears' preference for feeding only on fruits with mature seeds is probably due to the phenological change in the fruit. The fruit diameter increased following a double sigmoid growth curve (Fig. 2a), similar to that of drupes and other *Prunus* species (Ishii 1991). The endocarp of *P. jamasakura* started to harden at about day 32, during the second stage. As the endocarp hardens, the embryo and albumen mature, enabling the seed to germinate. During the third stage, the fruit color changed rapidly. The change in fruit color and the rise in sugar content may be due to changes in photosynthate concentrations directed by phytohormones produced when seeds mature (Okamoto 1996). During the third stage, the amount of edible fruit peaked and the sugar concentration rapidly increased. We assumed that the available energy in fruit peaks during the third stage.

We observed that bears fed on the *P. jamasakura* fruit mostly during days 58–62 and for about a month at a range of altitudes where fruit maturation was at its peak. The captive bear experiments showed that bears fed more on black fruits with high sugar concentrations than on green fruits with low sugar concentrations (Table 3). One reason for this might be that the bears intentionally select and feed on the *P. jamasakura* fruits becoming high nutrition because the previous studies reported that American black bears and brown bears select foods that are relatively high in nutrients and easy to digest (Mealey 1980; Herrero 1985)

Numbers of persisting fruits decreased rapidly after day 60 (Fig. 1c), but bears fed mostly during days 58–62 (Fig. 3). In this disappearance, most fruit that disappeared was classified as "fruit without pedicel"—that is, the pedicels remained attached to the tree. In contrast, all fruit with pedicel were discovered at the bases of the test trees. We have observed that when birds feed on

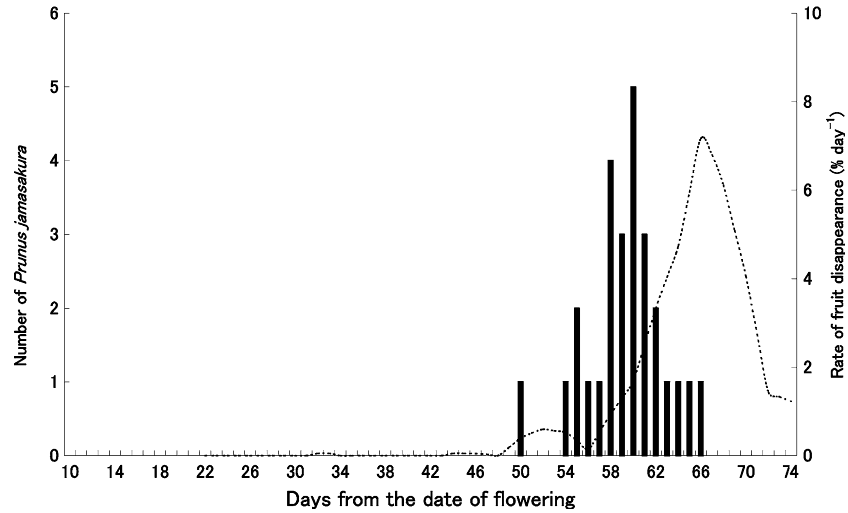

Fig. 3 Frequency of bear signs on *Prunus jamasakura* in the mountain site. Signs included claw marks on the trunk and stems and bear shelves in the trees. *Broken line* indicates the rate of fruit fall (“fruit without pedicel”) per day (Fig. 1c)

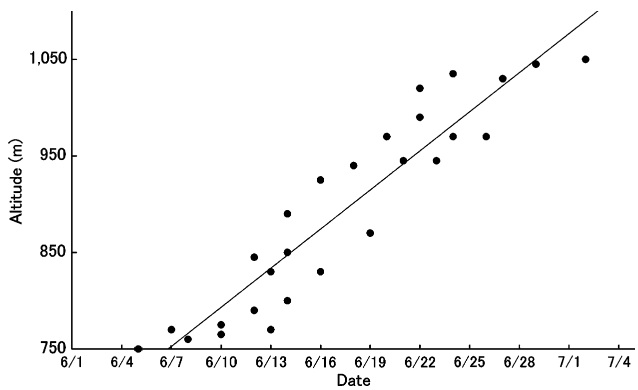

Fig. 4 Relationship between the date when bears marked trees in the mountain site and the altitude of the marked trees (n = 102, r^2 = 0.875, P < 0.001)

Table 2 Percentage of ingested fruits of two colors and apparently intact seeds during fruit maturation

Days after flowering	Fruit color	Ingested fruit (%)[b]	Apparently intact seeds (%)[c]
50	Green	6.7 ± 2.3	97.2 ± 3.1
	Red	91.7 ± 5.0	96.2 ± 2.3
55	Green	3.8 ± 1.5	96.5 ± 4.2
	Black	100	97.4 ± 3.1
60	Green	5.7 ± 1.6	97.2 ± 2.3
	Black	98.7 ± 1.2	99.3 ± 3.2
65	Green	4.0 ± 2.9	95.7 ± 4.2
	Black	100	96.8 ± 3.4
70	Green	6.7 ± 1.8	96.3 ± 3.2
	Black	100	98.6 ± 4.2
Seed from collected wild feces[a]			97.0 ± 11.8

[a] Data from Koike et al. (2003)
[b] Percentage of 100 green + 100 red (day 50 only) or black *P. jamasakura* fruits ingested
[c] As a percentage of the total number of seeds ingested

fruits of *P. jamasakura*, they leave the pedicels attached to the tree. Since the number of “fruit without pedicel” rapidly increased as the fruit ripened and pedicels remained, we deduced that birds were the major frugivores during this period. It is known from several studies that changes in color and a rapid increase in sugar levels are closely related to seed dispersal, resulting in a higher percentage of fruit removal (e.g., Ridley 1930; Willson and Thompson 1982). Moreover, most of the fruits dispersed by birds are red or black (Wheelright and Jansen 1985). Therefore, we assume that bears feed on the fruits of *P. jamasakura* earlier than other frugivores, when a large amount of fruits exist in the canopy.

Effect of bear ingestion on seed germination

P. jamasakura seeds found in the feces of captive bears were not damaged. Wild bears may rarely damage the seeds of any fleshy fruits, because the proportion of damaged seeds in the current study does not differ from that in our earlier study (Koike et al. 2003) (Table 3).

Ingestion by birds can enhance germination by modification of the structure of the seed coat (Agami and Wisel 1986). Although the gut passage time of bears (5–37 h) is much longer than that of birds (Fukui 2003, ca. 1 h), such enhancement by bears was not observed (Table 4). On the other hand, wrapped seed did not germinate at all, even though the viability of wrapped seeds did not significantly differ from that of ingested seeds or germinated exposed seeds. Therefore, it is likely that ingestion by bears can enhance germination by removing a germination inhibitor in the pulp (Ishii 1991).

Effectiveness of bears as seed dispersers

Schupp (1993) suggested that disperser effectiveness affects plant reproduction and has both quantitative and qualitative components. From the qualitative perspective, Asiatic black bears are effective dispersers of *Prunus* seeds for the following three reasons: first, the ingestion

Table 3 Percentage of germinated and viable ungerminated ingested, exposed, and wrapped seed during fruit maturation

Days after flowering	Germination percentage		
	Ingested seed[a]	Exposed seed	Wrapped seed
50	44.2 ± 3.3 (0)	46.7 ± 6.0 (0)	0.0 (47.5 ± 5.21)
55	61.0 ± 5.5 (0)	57.2 ± 4.2 (0)	0.0 (53.0 ± 7.2)
60	66.3 ± 7.3 (0)	59.8 ± 6.5 (0)	0.0 (57.3 ± 6.8)
65	66.2 ± 6.6 (0)	60.3 ± 4.5 (0)	0.0 (57.5 ± 5.5)
70	62.7 ± 6.4 (0)	62.3 ± 4.1 (0)	0.0 (57.2 ± 5.1)

Values in parentheses indicate percentages of viable ungerminated seed

[a] Only ingested red (day 50 only) or black fruit

of *P. jamasakura* fruits did not damage the seeds: second, ingestion removed the pulp, which might contain a germination inhibitor, without lowering the germinability; and third, the long gut-retention time (5–37 h) enabled the bears to disperse seeds far from the parent tree.

Quantitative effectiveness, however, cannot be fully tested by the data presented here. We have no data on visits by other dispersers or on the number of seeds dispersed per visit. Therefore, we cannot evaluate the quantitative effectiveness of bears as seed dispersers. Two crucial factors must be evaluated. The first is the fate of deposited seeds. Bears often drop thousands of seeds in one fecal deposit (Koike et al. 2003). This may attract postdispersal seed predators or may cause severe sibling competition among seedlings. The second is the quantity of dispersed seeds. Bears feed on large amounts of fruits, but the contribution of bears to the entire fruit production consumed is not known.

In Japanese deciduous forests, bears are considered umbrella species (Oi 2004), but the actual role of bears in forest ecosystems has not been fully elucidated. Our results indicate that bears adjust their feeding periods to obtain more energy from *P. jamasakura* fruits of individual trees, making them potentially effective seed dispersers from a qualitative point of view.

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