

Avian seed ingestion changes germination patterns of bilberry, *Vaccinium myrtillus*

Johanna Honkavaara*, Heli Siitari, Virpi Saloranta & Jussi Viitala

Department of Biological and Environmental Science, P.O. Box 35 (YAC), FI-40014 University of Jyväskylä, Finland (*corresponding author's e-mail: johanna.honkavaara@utu.fi)

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Frugivores functioning as seed dispersers may have fundamental effects on the reproductive success of fruiting plants. Studies on this interaction have, however, mostly ignored possible within-season and between-year variations in seed germination behaviour. The aim of this study was to assess how berry ingestion by thrushes (*Turdus* spp.) affects seed germination of bilberry (*Vaccinium myrtillus*). Specifically, we studied if the timing of dispersal within the fruiting season affects germination success of seeds and whether these effects vary between years. The germination rate of intact seeds declined in the course of the fruiting season both in 1997 and in 1999. Ingestion by thrushes accelerated the germination rate of passed seeds and the final germination percentages of passed seeds were higher than or similar to those of intact seeds. These effects varied within season and between years. Thus, when effects of frugivores on seed germination success are studied, experiments should not rely on the data collected at a single time in the season and in a single year.

Key words: germination patterns, gut passage, seed ecology, *Turdus* spp., *Vaccinium myrtillus*

Introduction

Interactions between fruiting plants and frugivores have been the focus of increasing interest during the past few decades (Traveset 1998 and references therein, Levey & Benkman 1999 and references therein). In temperate ecosystems, frugivores are omnivorous and fruit–frugivore interactions are supposed to be of diffuse evolutionary value, if any, to the evolution of fruit traits of fruiting plants. However, frugivores may be of considerable aid in the colonization of new habitats. In addition to the effects on spatial dis-

persal of seeds, ingestion by birds may also affect temporal dispersal, if germination is enhanced or delayed (Traveset 1998 and references therein, Traveset *et al.* 2001). Germination may also be reduced or remain unchanged after ingestion by birds (Crossland & Vander Kloet 1996, Traveset & Willson 1997). Thus, seed dispersers may have fundamental effects on reproductive success of fruiting plants.

Dormancy, i.e. dispersal in time, is a widespread phenomenon especially among seeds of temperate-zone plants (Villiers 1972). The timing of germination may have important fitness conse-

quences for a plant growing from a seed (Simons & Johnston 2000). The mechanisms used by seeds to terminate dormancy and initiate growth are expected to allow plants to select favorable habitats (Preston & Baldwin 1999). One explanation for changes in germination patterns due to avian ingestion is mechanical and/or chemical abrasion of the seed coat in the digestive tracts of birds. Such abrasion may affect the physiology of dormancy and seed viability (Vázquez-Yanes & Orozco-Segovia 1986).

If dormancy of a seed is broken e.g. too early by abrasion, a seedling may be doomed to vanish in unsuitable conditions (Janzen 1983). Thus gut treatment by frugivores should be sufficient to enable seed germination, but gentle enough to prevent premature breaking of dormancy (Smith 1975). Seasonality and its impact on the germination success of seeds and seedling establishment may further modify these interactions (Traveset 1998). The germination patterns of seeds collected at different times in the season might vary due to seed dormancy being at different stages (Baskin *et al.* 2000). There may also be between-year variation in these interactions.

Although the effects of frugivores on the germination success of fruiting plants were addressed in numerous studies (Traveset 1998 and references therein), in most cases the dormancy properties of species studied were not considered (but *see* Traveset *et al.* 2001).

Bilberry (*Vaccinium myrtillus*) is a clonal dwarf shrub common in Eurasian forest ecosystems. In Finland berries of *V. myrtillus* ripen from mid-July to the beginning of August, in approximately 50 days from the beginning of the flowering period (Vänninen *et al.* 1988). Bilberry seeds have nondeep physiological dormancy and they need cold-stratification to germinate at low temperatures (Baskin & Baskin 1998: p. 408, Baskin *et al.* 2000). Bilberries are rich in sugars and have no defence chemicals against seed predators and microbes. Such berries are supposed to benefit from quick removal by frugivores before they become over-ripe (Stiles 1980).

Bilberries are eaten by birds e.g. turdids and tetraonids, and also by mammals e.g. voles, foxes and bears. Sexual reproduction and seed dispersal by birds and mammals provides opportunity for recruiting new habitats over relatively

long distances as compared with clonal growth. In Finland, avian consumption of berries is at its highest soon after the main crop has matured (Laakso 1990), at the same time as young birds learn to forage and birds amass energy reserves for autumn migration (Stiles 1980). As many diurnal birds can detect UV light, the UV-reflective wax layer of bilberry may function as an effective advertisement to avian seed dispersers (Siitari *et al.* 1999).

In this study, our aim was to assess the effects of passing through the digestive tracts of birds on the seed germination success of bilberry, *V. myrtillus*. In particular, we were interested to study if the effects of birds on germination patterns vary within the fruiting season, i.e. if the timing of ingestion affects the results. In addition, we studied whether these effects vary between years. We used natural consumers of bilberry i.e. fieldfares (*Turdus pilaris*) and redwings (*Turdus iliacus*), which are abundant frugivorous turdids in northern Europe.

Material and methods

Collection of material

We collected bilberries from three different areas of *Vaccinium myrtillus*-type forest (classification from Kalela 1961) within 6 km of Konnevesi Research Station in central Finland (62°37'N, 26°20'E) in 1997 and in 1999. Since bilberry clones can be over five-meter wide (Jalas 1980: p. 298), we collected berries randomly from separate shoots at adequate distances from each other to assure that different clones were represented.

Unfortunately, we did not know the actual age of the berries, i.e. the length of the time the berries had been mature before collection. However, in central Finland practically all bilberries mature around the beginning of August depending on the cumulative heat sum (Vänninen *et al.* 1988, Laakso 1990). The berries remain attached to the shoots for many weeks, some even until late October (Laakso 1990). The appearance of the berries changes with aging, so the berries collected in early August had most probably quite recently matured. Berries collected in mid- and

late September had started to lose their turgor. Frugivorous birds in these experiments were juvenile fieldfares in 1997 and adult redwings in 1999. Fieldfare is migratory in northern parts of Europe, but may overwinter already in southern Scandinavia. Redwing nests in summer in Scandinavia and overwinters in western and southern Europe. Body mass of fieldfare is approximately 100 g and that of redwing is about 60–65 g. Both species forage mainly on worms and insects during the breeding season, and before migration they feed on fruits and berries.

We collected fieldfare broods (approximately 9–12 days old) with their nests and hand-raised them. These birds were also used in different behavioural experiments in 1997. We mistnetted adult redwings during reproductive season in 1999 (their brood was also collected and hand-raised for different behavioral experiments). We fed the chicks approximately every two hours until they learned to eat by themselves. We initially fed the birds with a food mixture containing minced meat, cottage cheese, salad, bread, dog food, apple, egg, extra vitamin and calcium (adjusted recipe from Helsinki Zoo, Finland). Also, we offered them meal worms (*Tenebrio molitor*). As the young birds grew up, we gradually changed their diet to include also minced dog sausage, cucumber and watermelon. Water was available *ad libitum*. The birds remained in good condition throughout the captivity period and were released back to nature after the experiments.

Experimental procedure

We repeated the experiments three times in 1997 and 1999. In 1997 we collected berries early in the fruiting season (early August: 7–14), at the end of the fruiting season (early September: 30 Aug.–4 Sep.) and after the fruiting season (late September: 20–24). In 1999 we performed the berry collection in late July (20–22), in the middle of August (17–18) and in the middle of September (10–12). We selected the fieldfares ($n = 12$) used in the feeding experiment randomly from 27 juveniles available in 1997. All the redwings we used ($n = 9$) in this experiment in 1999 were adults. We placed each bird alone

in an experimental cage. As fieldfares did not feed alone, the experimental cage was kept in the same room where all the birds were housed. During the experiment, each redwing was kept in a separate room. We offered individual fieldfares 20 berries per bird and redwing individuals five berries per bird on Petri dishes on the plastic floor of the experimental cage ($51.5 \times 21.5 \times 46.5$ cm). Redwings were given fewer berries than fieldfares due to their smaller body size and also because previous experience with fieldfares had shown that almost all seeds pass the digestive tract. After a bird had eaten all the berries, we waited four hours to ensure that most of the ingested seeds had passed through the bird's digestive tract.

The floor of the experimental cage was covered with water to wet the faeces and to ease the removal of passed seeds from the faeces. We collected the seeds with forceps and placed them on paper towels to dry. The seeds were incubated at 22 °C for four weeks, after which we moved them to plastic centrifuge tubes (1997) or placed them in plastic film containers (1999). To keep the seeds dry, we inserted cotton in the opening of the centrifuge tubes and placed the lids on the film containers. We kept the seeds for another four weeks at 4 °C for cold stratification. Moreover, we collected seeds which were used as a control (from here on referred to as intact seeds) from bilberries (number of berries from each collection: $n = 20$ in 1997 and in 1999). We gently broke the berries in a Petri dish filled with water and removed the seeds with forceps. At the same time we counted the number of seeds. We incubated and cold stratified the intact seeds using the same procedure as for the passed seeds. To avoid any effect of cool storage upon germination patterns, we processed all berries on the day of collection.

Germination procedure

We examined the seeds with a bioscope to select only undamaged and normally shaped seeds for germination trials. We germinated 200 randomly selected passed seeds per bird in 1997 and 100 in 1999. We used all fully shaped seeds collected from the berries as a control (there were approx.

49 ± 2.1 . S.E. seeds per berry). We sterilized all the equipment used in the germination study with 94% ethanol. We placed four layers of suction paper in each Petri dish used. On the top of the papers, we placed a plastic plate (10 × 10 cm) with 100 drilled holes (\varnothing 2 mm). We moistened the papers with 5 ml of distilled water and placed one seed in each hole. We placed the seeds collected from the berries or those collected from the faeces of individual birds on separate Petri dishes.

In 1997 we kept the Petri dishes in an indoor growing chamber at the Department of Biological and Environmental Science in Jyväskylä with six florescent tubes (Sylvania Gro-Lux F58W/GRO) as a light source. In 1999 we germinated the seeds in a growing chamber at Konnevesi Research Station's new research hall with two florescent tubes (Philips LTD 56W/860) as the light source. The temperature of the chambers was approximately 20 °C and the light rhythm was 12h:12h (light:dark). When necessary, we moistened the Petri dishes with distilled water, i.e. approximately every second day. We monitored the seeds for radicle emergence on the 14th, 20th and 26th days after the start of the germination experiment. We calculated the numbers of germinated seeds cumulatively, e.g. seeds germinated on the 14th and 20th days were also included in the count on the 26th day.

Statistical methods

We performed statistical analyses using SPSS 10.1.3 for Windows (SPSS Inc. 1989–2000). We used the arcsin-square root transformation due to proportional nature (i.e. values used were seed germination percentages) of the data. With a two-way ANOVA, we determined the effects of the treatments (passed or intact seeds) and the time of seed collection (three separate dates per year, please *see* 'Experimental procedure') on the germination success at three control dates (14, 20 and 26 days after the start of germination experiment), respectively. Due to significant treatment effects and interaction, further testing was carried out separately within each treatment or within each time of seed collection. For the last control date (i.e. 26 days), no interaction was found and

thus further tests were not performed. To locate the differences among times of the seed collection within intact or passed seeds, we used a one-way ANOVA with the Bonferroni post-hoc test. We used an independent samples *t*-test (adjusted with sequential Bonferroni technique, *see* Rice 1989) to locate differences among treatments (passed and intact seeds) separately within each time of seed collection. We analyzed separately the data collected in 1997 and in 1999, because there was a slight difference in methodology, i.e. in light conditions in the chambers, which might have affected the results.

Results

For both years of the research, the germination rate differed between the two treatments (intact and passed seeds) and between the times of seed collection (Figs. 1 and 2; Table 1). On the 14th day after the start of the germination experiment in 1997, the germination rate of the intact seeds declined in relation to the duration of the fruiting season (Fig. 1a–c; Table 2). The change during the season in germination percentage differed between treatments (Table 1), as the germination rate of passed seeds remained similar throughout the season (Table 2). The germination rates were higher for passed than for intact seeds (Table 1) excepting seeds collected earliest in the season i.e. early August (Table 3).

In 1999, germination rates on the 14th day differed between treatments and between different seed collection times within the season. There was also variation in this effect between treatments (Table 1) (Fig. 2a–c). The germination rates did not differ between treatments for the seeds collected in late July, but for the seeds collected at other times in the season the passed seeds had higher germination rates (Table 3). For passed seeds, the germination rate on the 14th day was lower in the middle of September than at other times of the season. For intact seeds, the germination rate was higher in late July than in the middle of August and in the middle of September (Table 2).

Both in 1997 and 1999, the germination success after 20 days differed between treatments (Table 1). In 1997, there was also variation in

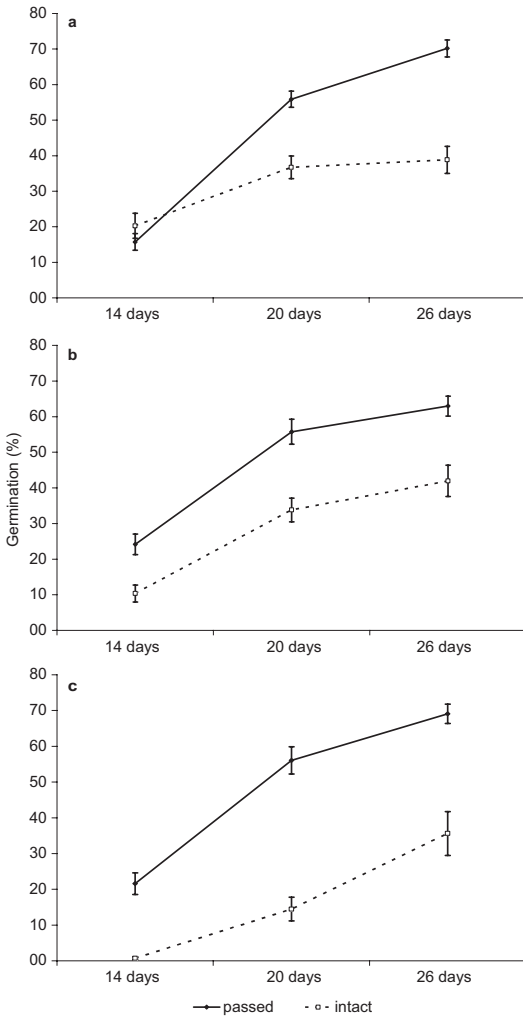


Fig. 1. Mean germination percentages (\pm S.E.) of intact and bird-ingested (passed) bilberry seeds collected in (a) early August, (b) early September and (c) late September in 1997.

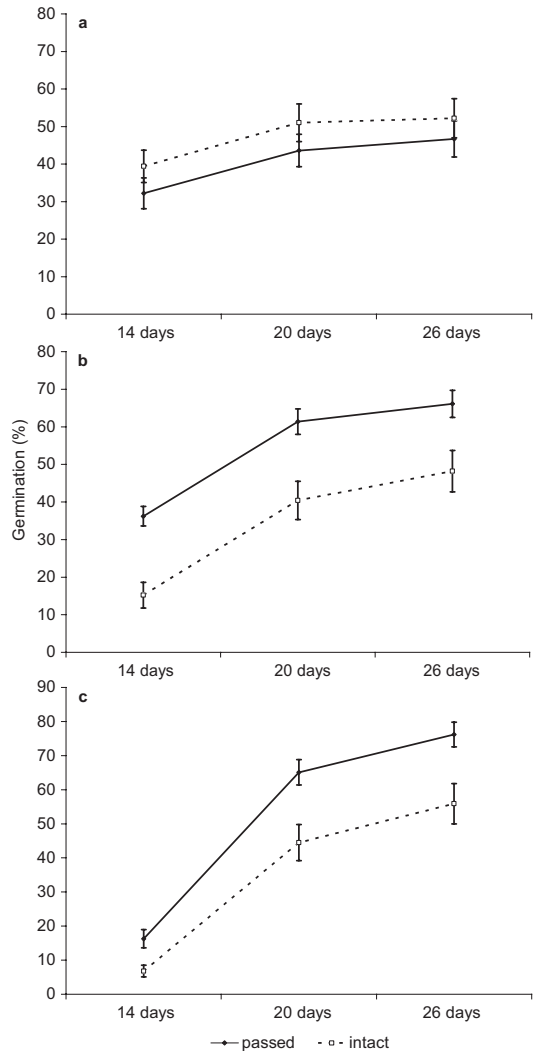


Fig. 2. Mean germination percentages (\pm S.E.) of intact and bird-ingested (passed) bilberry seeds collected in (a) late July, (b) the middle of August and (c) the middle of September in 1999.

Table 1. The effects of gut passage and time of seed collection within the fruiting season on bilberry seed germination percentages 14, 20 and 26 days after the start of the germination experiment conducted in 1997 and in 1999.

Variable	df	F (14 days)	F (20 days)	F (26 days)
1997				
Treatment	1,81	38.65***	85.01***	59.47***
Time of seed collection	2,81	10.17***	7.71**	0.19 ^{n.s.}
Interaction (treatment \times time)	2,81	19.39***	7.97**	1.10 ^{n.s.}
1999				
Treatment	1,79	9.44**	4.76*	3.07 ^{ns}
Time of seed collection	2,79	17.64***	0.97 ^{ns}	3.93*
Interaction (treatment \times time)	2,79	6.25**	3.85*	2.57 ^{n.s.}

n.s. = not significant (i.e. $p > 0.05$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

the germination success during the season and the treatments differed in this variation (Table 1) (Fig. 1a–c). The passed seeds had higher germination percentages than intact seeds (Table 3). The germination success of intact seeds varied, as the proportion of seeds germinated on the 20th day was lower for seeds collected in late September than for seeds collected at other times

in the season (Table 2). In 1999, the passed seeds germinated faster than intact seeds (Table 1) except the seeds collected in late July (Table 3). The germination on the 20th day did not differ during the season (Table 1), even though the passed seeds collected in late July germinated more slowly than the seeds collected at other times in the season (Table 2) (Fig. 2a–c).

Table 2. The effect of seed collection time within the fruiting season on germination success of passed and intact bilberry seeds (one-way ANOVA with Bonferroni post-hoc test) in the germination experiment conducted in 1997 and in 1999.

	Days after germination	Treatment	df	<i>F</i>	Post-hoc comparisons between times of seed collection
1997	14 days	passed	2,30	2.70 ^{n.s.}	–
		intact	2,51	27.48 ^{***}	early August–early September* early August–late September ^{***} early September–late September ^{***}
	20 days	passed	2,30	0.002 ^{n.s.}	–
		intact	2,51	14.64 ^{***}	early August–early September ^{n.s.} early August–late September ^{***} early September–late September ^{***}
1999	14 days	passed	2,22	10.99 ^{***}	late July–middle of August ^{n.s.} late July–middle of September ^{**} middle of August–middle of September ^{**}
		intact	2,58	25.42 ^{***}	late July–middle of August ^{***} late July–middle of September ^{***} middle of August–middle of September ^{n.s.}
	20 days	passed	2,23	9.90 ^{**}	late July–middle of August ^{**} late July–middle of September ^{**} middle of August–middle of September ^{n.s.}
		intact	2,56	1.27 ^{n.s.}	–

n.s. = not significant (i.e. $p > 0.05$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Table 3. The effect of bird ingestion on seed germination of bilberry at different seed collection times within the fruiting season. Pairwise comparisons of passed and intact seeds were performed with the independent samples *t*-test on the control dates separately (corrected with sequential Bonferroni technique, see Rice 1989).

	Time of seed collection	Days after germination			
		14		20	
		df	<i>t</i>	df	<i>t</i>
1997	Early August	30	–0.805 ^{n.s.}	29.799	4.862 ^{***}
	Early September	28	3.724 ^{**}	28	4.017 ^{***}
	Late September	16.165	10.151 ^{***}	23	6.935 ^{***}
1999	Late July	26	–0.966 ^{n.s.}	27	–0.983 ^{n.s.}
	Mid-August	25.946	5.096 ^{***}	26.979	3.39 ^{**}
	Mid-September	25	2.746 [*]	24.525	2.856 [*]

n.s. = not significant (i.e. $p > 0.05$), * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

In both 1997 and 1999, the final germination percentages (i.e. germination percentages at 26th day) did not vary due to the time of the seed collection between treatments (Table 1). In 1997, the final germination percentages were not affected by the time of seed collection (Table 1) and were higher for passed seeds than for intact seeds (Independent samples *t*-test: $t = 9.1$, d.f. = 81.04, $p < 0.001$). In 1999, the time of seed collection only slightly affected final germination percentages (Table 1), as the final germination percentage tended to be lower for seeds collected in late July than for seeds collected in the middle of September (Bonferroni: for all comparisons n.s.) (Fig. 2). In 1999, the final germination percentage did not differ between intact and passed seeds.

Discussion

The germination rate of the intact seeds declined over the course of the fruiting season. Bird-ingested seeds germinated faster and also had a final germination percentage higher than or similar to that of intact seeds. However, these effects of ingestion by birds varied within the season and between the study years. These results implicate that the effect of frugivores on seed germinability and germination rate may vary depending on the time of the fruiting season when the berries are ingested and their seeds are dispersed.

Changes in the state of conditional dormancy (the first phase of dormancy loss in nondeep physiological dormancy; Baskin & Baskin 1998: p. 50) in developing bilberry seeds might explain the decline in germination rate of the intact seeds during the season. It is also possible that some seeds were still dormant after 26 days. Some of the ungerminated seeds might have been unviable in both treatments (intact and passed seeds). However, we assume that the error caused by unviability was similar in both treatments. Gut passage did not negatively affect germinability or germination rate, thus the viability of the seeds was probably not diminished.

Baskin *et al.* (2000) collected bilberry seeds from southern Sweden during a fruiting season on four separate dates and sowed them dried but not cold-stratified in pots kept in a greenhouse.

Part of the seeds sown earliest in the fruiting season (29 July and 5 Aug.) germinated already during the same growing season. However, the seeds sown later in the season (19 Aug. and 3 Sep.) did not germinate until the next summer. Baskin *et al.* (2000) also studied the effects of various combinations of stratification, light and temperature conditions on germination patterns in the laboratory. According to their results, germination patterns of bilberry can vary considerably due to environmental conditions and seeds need cold stratification to germinate at low temperature regime of 15:5 °C (12h:12h).

The observed acceleration of the germination rate by birds may be due to changes in the dormancy properties of seeds. Chemical and/or mechanical abrasion of the seed coat during gut passage could shorten conditional dormancy in bilberry and thus result in hastened detection of germination cues. Furthermore, abrasion may have diminished physical restriction of the seed coat (so-called functional dormancy) and thus decreased embryo growth needed to break the covering structures. Undamaged coats of intact seeds may be less permeable to gases and water compared to ingested seeds (Traveset 1998 and references therein). This might delay germination of some seeds, explaining slower germination rate of intact seeds. However, in species with nondeep physiological dormancy the exact mechanism of dormancy probably varies, although the best explanation for its operation might be an interaction between the embryo and its covering structures (Baskin & Baskin 1998: p. 33). Thus, further studies are needed to confirm the mechanism behind the effects of bird ingestion on the germination patterns of bilberry seeds.

In a study on North American blueberry (*V. angustifolium*) seed passage through American robins' (*Turdus migratorius*) guts resulted in reduction of the total germination percentage. However, germination rate did not differ between intact and passed seeds (Crossland & Vander Kloet 1996). On the other hand, seed ingestion by two different thrush species, the American robin and the varied thrush (*Ixoreus naevius*), had no effect on the germination patterns of *Vaccinium ovalifolium* and *V. alaskaense* seeds (Traveset & Willson 1997). In both studies, seeds were sown

early in the fruiting season. Interestingly, fresh *V. angustifolium* seeds germinated readily in the laboratory, whereas seeds of *V. ovalifolium* and *V. alaskaense* were planted outdoors and did not germinate until next summer. Species-specific differences in germination patterns or lack of stratification (Baskin *et al.* 2000) in the former study may have caused negative impact of gut ingestion on germinability (Crossland & Vander Kloet 1996).

Like Traveset and Willson (1997), we also used two thrush species, the redwings and fieldfares. The birds were kept on similar diet in captivity and the retention time (i.e. seed passage time after ingestion) for both species is about two to three hours (J. Honkavaara pers. obs.). Thus, as the germination patterns of intact seeds also varied between years, the between-year variation in the effects of gut passage is probably due to e.g. environmental effects during maturation on seed germination patterns rather than due to between-species differences in seed treatment.

In general, seeds germinating soon after the start of the growing season might result in a higher proportion of successfully established seedlings (Simons & Johnston 2000, Paulsen & Högstedt 2002). Eriksson and Fröberg (1996) sowed bilberry seeds in the field in southern Sweden in August and found seedlings emerging throughout the next growing season, although most of them emerged early in the growing season. All the surviving seedlings had germinated during the first summer after sowing. Ericson (1977) reported similar results. However, as conditions for the establishment of a plant differ from conditions for germination (Turnbull *et al.* 2000), assessment of the ecological significance of germination enhancement by bird-ingestion would demand further research into the post-dispersal fate (Bustamante *et al.* 1993, Schupp 1995) of ingested bilberry seeds.

The berry and seed production in the genus *Vaccinium* stands are often very high. This is paradoxical in the light of the rarity of seedlings and paucity of seed bank (Vander Kloet & Hill 1994). Indeed, successful habitat recruitment from seeds among clonal shrubs is rare for bilberry (Eriksson & Ehrlén 1992), as bilberry is unable to germinate among undisturbed vegetation (Ericson 1977). However, establishment of new genotypes is pos-

sible on small disturbances (Eriksson & Fröberg 1996, Hautala *et al.* 2001). Thus, bilberry may be able to recruit at “windows of opportunity”, i.e. spatially or temporally unpredictable conditions in which seedling recruitment is possible among established conspecific adults (Eriksson & Fröberg 1996). As bilberry recruitment is microsite and seed limited (Eriksson & Ehrlén 1992), efficient seed dispersal is crucial for finding these “windows of opportunity”. In genus *Vaccinium*, seed dispersal traits are probably evolutionarily ancestral relative to clonal growth form (Eriksson 1992). Eriksson (1992) suggests that clonal propagation may have been augmented in order to make genet fitness less dependent on local dispersal by seeds.

Our study focused on the effects of avian ingestion, as our aim was also to assess the possibility of within-season and between-year differences in germination patterns of bilberry. In Finland, bilberries are also eaten by at least 14 mammalian species (Siivonen 1972). Traveset and Willson (1997) found gut passage through bears to have no effect on the germination success of *V. ovalifolium* or *V. alaskaense* seeds. However, large droppings with thousands of seeds may not be optimal germination sites due to severe competition and mortality (Traveset & Willson 1998). Hickey *et al.* (1999) found that the seeds of these *Vaccinium* spp. passed through the guts of the American marten (*Martes americana*) and remained viable. They suggest that omnivorous predators may function as effective seed dispersers. Small rodents, like voles, also consume a substantial part of the bilberry crop (Laakso 1990) and while they are mainly seed predators (Honkavaara 1997), they may also disperse some seeds (Ericson 1977). The effects of different mammalian species on seed dispersal and seed germination patterns of *Vaccinium* spp. clearly demand further study.

In conclusion, this study delivers new insights to research on the germination of bird-dispersed species in seasonal environments. According to our results, potential within-season variation, e.g. changes in dormancy patterns, and between-year variation might influence the results of germination experiments, and thus affect interpretations of the effects of different seed disperser taxa on a plant's reproductive success. We suggest that

research on temperate fruit–frugivore interactions should not rely on data collected at a single time in the season and in a single year.

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