Effect of birds and bears on seed germination of fleshy-fruited plants in temperate rainforests of southeast Alaska

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The effects of avian and mammal seed dispersers on seed germination were investigated for six common plant species (five shrubs and one herb) in the temperate rainforests of southeast Alaska. Patterns of germination behaviour were compared between defecated seeds and control (unpassed) seeds for a period of two years. Seed passage through vertebrate frugivores enhanced germination in two species, *Rubus spectabilis* and *Sambucus racemosa*, and a similar trend was observed in *Ribes bracteosum*. In contrast, it did not affect seed germination in *Oplopanax horridus*, *Streptopus amplexifolius* and *Vaccinium ovalifolium/alaskaense*. No differences in germination behaviour were found between bear- and bird-treated seeds, suggesting that seed retention time (much greater in bears than in birds) in the guts does not relevantly affect germination. Differences among frugivore effects were detected only for *Sambucus*, with varied thrushes enhancing germination more than American robins and black bears. The two colour morphs of *Rubus spectabilis* showed similar germination patterns, suggesting that seed dispersers do not exert an important selective pressure contributing to the maintenance of the polymorphism, at least through the mechanism of a differential effect on germination.
The results of this study support the idea that the advantages of animal seed dispersal lie more in seed movement away from the parent plant than in seed treatment within the disperser's guts.

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Frugivorous animals that act as seed dispersers usually consume the pulp and regurgitate or defecate all or some of the seeds intact (unharmed) (Ridley 1930). Besides transporting the seeds away from the parent plant to safe sites for future germination and seedling growth, seed dispersers can also have an important influence on the time of germination and on germination success (percentage of seeds that germinate). Such influence is usually attained by 1) removing the fruit skin and pulp and thus the germination inhibitors that may be present in them (Evenari 1949, Mayer and Poljakoff-Mayber 1975, Izhaki and Safriel 1990, Barnea et al. 1991, Witmer and Cheke 1991), as well as reducing microbial or fungal attack (Ng 1983, Jackson et al.

1988); 2) a mechanical or chemical scarification of the seed coat (Barnea et al. 1990, Izhaki and Safriel 1990); and/or 3) by killing a fraction of the seeds ingested (e.g. Izhaki and Safriel 1990 and references therein).

Seed treatment within the guts of seed dispersers is one of the qualitative aspects that needs to be considered when determining the "effectiveness" (sensu Schupp 1993) of such dispersers. Nevertheless, relative to the great number of studies carried out in many different environments on other ecological and evolutionary aspects of frugivory and seed dispersal, little attention has been paid to the germination response of seeds after passing through digestive tracts. Enhancement of germination (higher percent or faster

Species (Family)	Fruit colour	Fruit diam. (mm)	Number of seeds per fruit			
			N	$\bar{X}$	SD	range
Rubus spectabilis (Rosaceae)	red/orange	20-25	42	43.9	4.5	25-69
Sambucus racemosa (Caprifoliaceae)	red	4-5	20	2.2	0.7	1-3
Ribes bracteosum (Saxifragaceae)	purple-blue*	6-10	18	12.3	8.0	3-31
Streptopus amplexifolius (Liliaceae)	dark red-purple	7-9	18	22.1	4.4	13-28
Oplopanax horridus (Araliaceae)	red	3-4	20	2.0	0.3	1-3
Vaccinium spp.[1] (Ericaceae)	blue	6-10	35	42.6	24.5	12-103

* with a white 'bloom' that probably reflects UV light.
[1] *ovalifolium* and *alaskaense*.

rate) has classically been stated to be a principal advantage of seed ingestion by frugivorous animals (Krefting and Roe 1949, Van der Pijl 1972), and many studies have found that defecated or regurgitated seeds germinate better than control (uningested) seeds, at least in some species (e.g. Lieberman and Lieberman 1986, Lieberman et al. 1987, Barnea et al. 1990, 1991, Izhaki and Safriel 1990 and references therein, Bustamante et al. 1992, Clergeau 1992, Ellison et al. 1993, Figueiredo 1993, Murray et al. 1994, Izhaki et al. 1995) and in some fruit-colour morphs (Willson and O'Dowd 1989). However, no evidence of germination enhancement has been found in many other species (e.g. Lieberman et al. 1979, Debussche 1985, Lieberman and Lieberman 1986, Braun and Brooks 1987, Barnea et al. 1992, Izhaki et al. 1995). Only in a few studies has seed ingestion by animals been found to lower the percentage of seeds germinating shortly after defecation (Livingston 1972, Smith 1975, Valido and Nogales 1994, Nogales et al. 1995, Crossland and Vander Kloet 1996) or to delay germination (McDiarmid et al. 1977, Ellison et al. 1993, Nogales et al. 1995).

We examined the effect of gut passage on seed germination behaviour of six species whose fruits are consumed by both birds and bears in the temperate rainforests of southeast Alaska. We discuss ecological and evolutionary implications for the plants of seed passage through guts of both classes of vertebrates. While birds have been studied extensively, the effect of mammals on seed germination has received much less attention (but see Applegate et al. 1979, Lieberman et al. 1979, 1987, Bustamante et al. 1992, Figueiredo 1993, Figueiredo and Perin 1995, Mandujano et al. 1994, Izhaki et al. 1995, and Nogales et al. 1995). The unique aspects of this study are: (1) it is the first to compare these two different groups of seed dispersers (birds and bears), and (2) it is the first that examines the effect of vertebrates on seed germination in this type of ecosystem.

Materials and methods

From mid-July to the beginning of August of 1993, ripe fruits of six fleshy-fruited plants were collected near Juneau, Alaska. Fruits of each species were collected from 10-20 individuals to gather as much variation as possible in germination responses. The species were salmonberry (*Rubus spectabilis*) (both red and orange berries were collected and considered separately in this polymorphic species), elderberry (*Sambucus racemosa*), stink currant (*Ribes bracteosum*), clasping twisted-stalk (*Streptopus amplexifolius*), devil's club (*Oplopanax horridus*), and blueberry (*Vaccinium ovalifolium* and *alaskaense*; these species hybridize and it is often difficult to discriminate between them). The main fruit characteristics for all these species are given in Table 1. A fraction of the collected fruits was fed to three American robins (*Turdus migratorius*) and to three varied thrushes (*Ixoreus naevius*) that were kept in an aviary in order to get the seeds from their droppings. Fruits were given to the birds along with a diet consisting of cat-food pellets, earthworms, and artificial fruit made of banana mash (Denslow et al. 1987). Seeds were recovered from the cages a few hours after defecation and were pooled for each bird species. Another fraction of fresh fruits was taken to the zoo in Anchorage, Alaska, and fed to both brown bears (*Ursus arctos*; two individuals) and black bears (*Ursus americanus*; four individuals). The bear dung was collected for a three-d period, kept in individual plastic bags in a refrigerator and taken to the lab in Juneau. Seeds were extracted within a week of being defecated. All these animals were previously known to disperse the seeds of the tested plants (MFW unpubl.).

A maximum of 500 seeds of each plant species (and of each morph in the case of *R. spectabilis*) was sorted from both bird and bear droppings after passing them

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through a sieve with running water. We similarly extracted seeds directly from fruits to get a control group of 500 seeds of each species that had not passed through the animals' guts.

A balanced experimental design was not possible because of the difficulties of getting enough seeds of certain species that were seldom eaten by the caged birds (*Ribes* and *Streptopus* for varied thrushes, *Oplopanax* for both bird species). Captive brown bears ate *Sambucus* fruits (AT pers. obs.), but no passed seeds were recovered, presumably because some droppings were missed in the large cages where these animals are kept. Brown bears may not feed upon *Sambucus* very often, judging from the low frequency of such seeds found in their scats on Chichagof Island, Alexander Archipelago, southwestern Juneau (MFW unpubl.).

All seeds were planted between August 13–18, 1993, in potting soil in 9-cm pots, the pot being the unit of replication. In most cases, five pots with 100 seeds each were used for each species and for each of the five treatments: a) robins, b) varied thrushes, c) brown bears, d) black bears and e) controls (unpassed). When fewer than 500 seeds were available, the number of seeds per pot was smaller. In the case of *Oplopanax* seeds passed through bird guts, the 100 seeds were split in five groups of 20 seeds. In the case of *Ribes* and *Streptopus*, only 100 and 350 seeds, respectively, were obtained from varied thrushes' scats. *Ribes* seeds were planted in two pots with 50 seeds each, whereas the *Streptopus* seeds were planted in four pots: three with 100 seeds and one with 50 seeds. Another set of 500 seeds of *Vaccinium, Rubus, Ribes* and *Oplopanax* were extracted from fresh scats of wild brown bears (the only species of bear) on Chichagof Island and planted in five pots (100 seeds/pot). Seeds were lightly covered with a thin layer (ca 2 mm) of potting soil.

All pots were randomly distributed in three 91 × 61 cm trays. The trays were covered with a 1-cm mesh lid to prevent seed predation by rodents and were placed together in the forest. The trays were surrounded by a fence to keep out deer and other possible animal disturbances.

Seeds were checked for germination from 3 May through 30 September the first year (1994) and from 2 May through 30 June the second year (1995), at intervals of 7–15 d. All seedlings were removed as they were being counted from each pot.

Repeated-measure analyses of variance (RM-ANOVA) were used to test for differences in germination rates among treatments for each species (in the case of *Rubus*, a two-way RMANOVA was performed using treatment and morph as main effects). Given that the number of seeds planted for each species was not constant, the proportion of seeds that germinated from each pot was the independent variable. Such proportions were arcsine transformed before the analyses in order to normalize the data. Final proportions of germinated seeds were compared among treatments with one-way ANOVAs.

Results

Germination of *Rubus spectabilis*

The patterns of germination of salmonberry seeds varied with treatments ($F_{4,40} = 3.46$, $P = 0.02$) but did not differ between the two colour morphs ($F_{1,40} = 1.18$, $P = 0.29$; treatment × morph not significant; time × treatment interaction $F_{88,880} = 2.21$, $P = 0.0001$; time × morph not significant). A slight difference between the two morphs was observed only for the robin treatment; germination rate tended to be greater for orange berries than for red ones (see in Traveset and Willson 1997: Fig. 2). For both morphs, passage through a consumer's gut enhanced germinaton (Fig. 1), that is, ingested seeds germinated at a higher rate than control (unpassed) seeds. However, the final proportion of germinated seeds was similar in all treatments ($F_{4,40} = 1.46$, $P = 0.23$) and in the two morphs ($F_{1,40} = 1.48$, $P = 0.23$; no significant interaction).

A separate analysis comparing germination patterns between seeds passed through wild brown bears (from Chichagof Island) and seeds ingested by captive brown bears showed no significant differences between them ($F_{1,13} = 0.55$, $P = 0.47$; time × treatment not significant). Average final seed germination was 53% and 60% for wild and captive brown bears, respectively ($F_{1,13} = 0.76$, $P = 0.40$).

Germination of *Sambucus racemosa*

Elderberry seeds passed through animals germinated faster ($F_{3,16} = 19.72$, $P = 0.0001$; time × treatment $F_{66,352} = 1.53$, $P = 0.009$) than controls, and final percent germination also differed greatly between treatments ($F_{3,16} = 20.44$, $P = 0.0001$) (Fig. 1). Varied thrushes enhanced germination more than robins and black bears (Tukey's test): by 30 June 1995, a total of 31% of the seeds ingested by varied thrushes had germinated (Fig. 1) in contrast to only 14% and 19% of the seeds ingested by black bears and robins, respectively.

Germination of *Ribes bracteosum*

Although seeds ingested by frugivores tended to germinate faster than controls (Fig. 1), the differences among treatments were not found to be significant in the RMANOVA ($F_{4,17} = 1.41$, $P = 0.27$; time × treatment $F_{88,374} = 2.03$, $P = 0.0001$). Final proportions of germinated seeds were also higher for passed seeds (the maximum being 64% in the robin treatment) than for
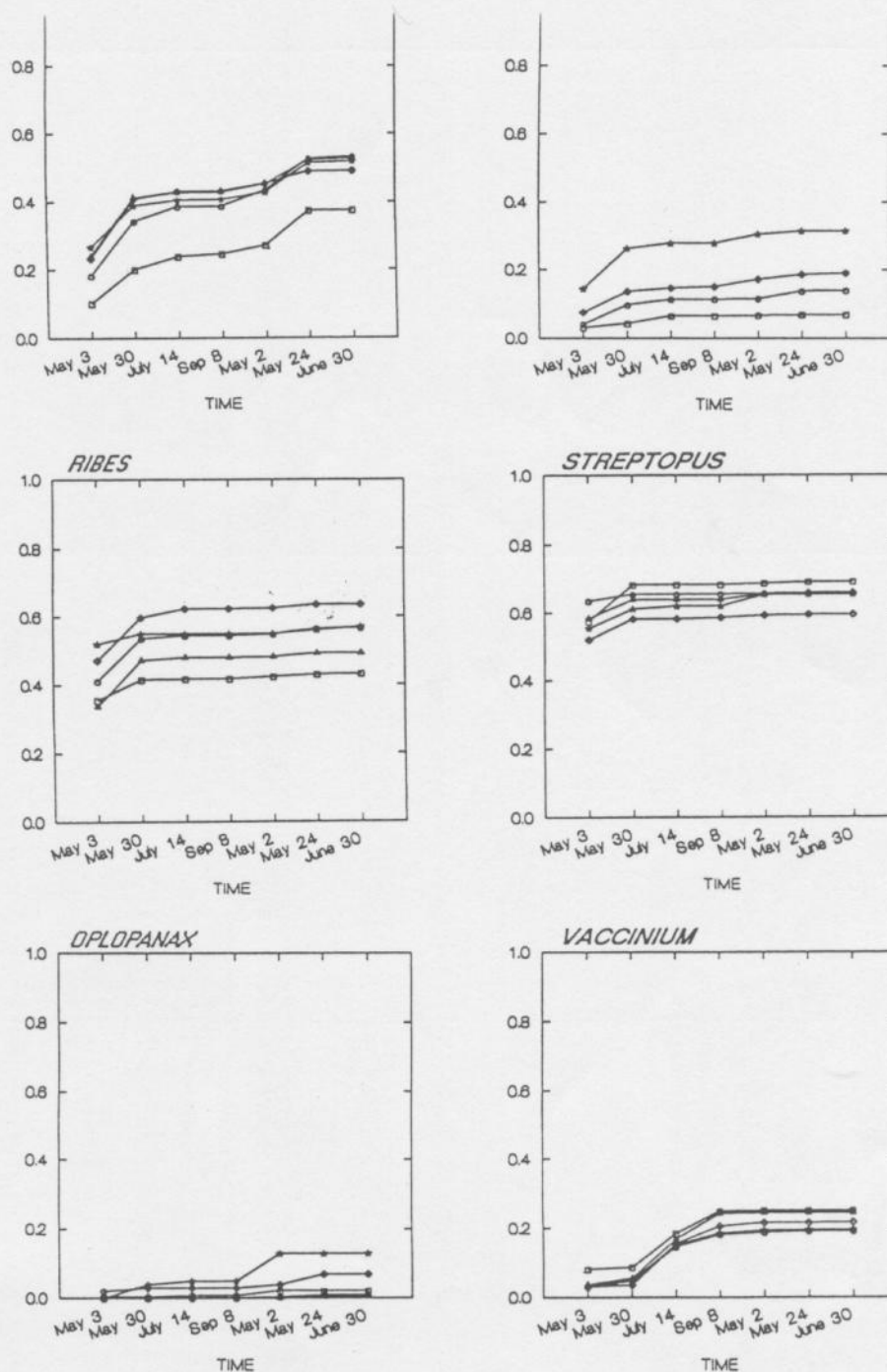
Fig. 1. Germination patterns (proportion of seeds germinating) of the six plant species studied. Germinations were recorded from 3 May through 30 September the first year (1994) and from 2 May through 30 June the second year (1995), at intervals of 7–15 d. ★ Varied thrush, ◇ American robin, △ brown bear, ○ black bear, □ control (unpassed seeds).

control seeds (43%), though the difference was not statistically significant ($F_{4,17} = 1.54$, $P = 0.24$).

Seeds passed through wild brown bears in Chichagof

Island germinated at a lower rate ($F_{1,8} = 11.86$, $P = 0.009$; time × treatment $F_{22,176} = 4.51$, $P = 0.0001$) and had a lower final percent germination (22% vs 49%;

$F_{1.8} = 11.11$, $P = 0.01$) than seeds passed through captive brown bears.

Germination of *Streptopus amplexifolius*

This species showed the highest rates of germination (Fig. 1) but this was so regardless of seeds being ingested by frugivores or not ($F_{4.19} = 0.37$, $P = 0.83$; time × treatment interaction $F_{88.418} = 1.68$, $P = 0.0004$) (Fig. 1). Final proportion of germinated seeds was similar for all treatments ($F_{4.19} = 0.33$, $P = 0.85$), ranging from 60 to 70%.

Germination of *Oplopanax horridus*

Very low (<2%) germination was observed in this species both during 1994 and 1995 (Fig. 1). Seeds treated in the digestive systems of either bears or birds did not germinate faster than unpassed seeds ($F_{4.20} = 1.40$, $P = 0.27$; time × treatment not significant). Likewise, although the final percent germination was 13% (varied thrush treatment) and the minimum was 0.4% (brown bear treatment), differences in this variable among treatments were not significant ($F_{4.20} = 0.96$, $P = 0.45$).

Oplopanax seeds ingested by wild brown bears in Chichagof showed a similar germination rate ($F_{1.8} = 0.40$, $P = 0.55$; time × treatment not significant) than seeds defecated by captive brown bears. Final germination was equally low (0.4%) for both treatments ($F_{1.8} = 0.40$; $P = 0.55$).

Germination of *Vaccinium ovalifolium/alaskaense*

Blueberry seed germination was not affected by passage through frugivores' digestive tracts (Fig. 1). Germination rate was similar among all treatments, including the two controls (*V. ovalifolium* and *V. alaskaense*) ($F_{5.24} = 1.12$, $P = 0.38$; time × treatment not significant). Most germination occurred during summer of the first year. By the end of the experiment, only a small fraction of the seeds (less than 25%, on average) had germinated and did not differ among treatments ($F_{5.24} = 0.78$, $P = 0.57$; Fig. 1).

As it happened with the seeds of *Ribes bracteosum*, blueberry seeds from Chichagof Island ingested by brown bears germinated at a much lower rate than seeds from the Juneau area ingested by captive brown bears ($F_{1.8} = 11.54$, $P = 0.009$). Final germination was on average 9% for the seeds from Chichagof while it was 24% for the seeds passed through captive bears ($F_{1.8} = 10.95$, $P = 0.01$).

Discussion

Enhanced germination success of seeds that are ingested by vertebrate frugivores has been documented for a long time in numerous studies, both for avian-seed dispersal sytems (e.g., Krefting and Roe 1949, Noble 1975, Temple 1977, Holthuijzen and Sharik 1985, Barnea et al. 1990, 1991, Izhaki and Safriel 1990, Clergeau 1992, Murray et al. 1994, Izhaki et al. 1995) and for mammal-seed dispersal ones (e.g., Lamprey et al. 1974, Applegate et al. 1979, Fleming and Heithaus 1981, Lieberman and Lieberman 1986, Lieberman et al. 1987, Utzurrum and Heideman 1991, Bustamante et al. 1992, Figueiredo 1993, Figueiredo and Perin 1995). Nonetheless, such enhancement is not universal, and many other studies find no effect or even a negative effect of seed ingestion on germination (references in introduction). The results of the present study add to such variation in germination responses. Vertebrate frugivores significantly increased germination in two (*Rubus* and *Sambucus*) of the six species examined; a similar but nonsignificant trend was observed in *Ribes*, while the rest of the species (*Streptopus*, *Oplopanax* and *Vaccinium*) was not affected by them.

The digestive tract of a given frugivore, either bird or bear, was found to have different effects on seed germination depending upon the species ingested. This has also been documented in other studies that investigate the effect of a fruit consumer on different plant species (e.g. Barnea et al. 1990, 1991, Izhaki and Safriel 1990, Clergeau 1992, Ellison et al. 1993). Several factors, not mutually exclusive, might account for such differences: (1) seed size, (2) seed coat thickness, (3) chemical content of the fruit pulp (these three factors intrinsic to the plant), and (4) nutrient composition of the food ingested along with seeds (extrinsic to the plant). Other factors such as presence of grit in bird gizzards (Clergeau 1992), chemical characteristics of the soil, and presence of pathogens in the feces and/or soil might well have different effects on different seed species, although this has not yet been documented.

Seed size has been shown to affect seed retention time in the guts – smaller seeds are voided more rapidly (e.g., Levey and Grajal 1991) – which in turn may influence germination. Several studies report that a longer retention in the guts translates into a lower germination (e.g., Janzen 1982, Murphy et al. 1993, Murray et al. 1994; but see Barnea et al. 1991 and Clergeau 1992). In the present study, no seed size effect was detected; the species with the smallest seeds (*Vaccinium* spp.) germinated about the same time as the other species in any of the treatments.

The thickness of the seed coat, quite variable among species, may determine the seed treatment inside the guts and consequently affect germination (e.g., Barnea et al. 1990, Izhaki et al. 1995); seeds with thick coats may need a longer retention time in order to be

Oplopanax have the thickest. The fact that the germination rate of *Streptopus* is so high (compared to the other species) might well be related to such thin coat.

The chemical content of the pulp has recently been shown to affect seed germination after passage through the disperser's guts. Murray et al. (1994) have reported that the presence of (undetermined) "laxative" chemicals in the fruit pulp of *Witheringia solanaceae* lowers seed retention time in the guts and that seeds voided rapidly are far more likely to germinate than those remaining longer in the disperser's gut. An alternative explanation, however, is that nutrient concentration of foods influences seed passage rate (Witmer 1996): for instance, low sugar concentrations have been found to decrease seed retention times in *Turdus migratorius*, *Hylocichla mustelina* and *Bombycilla cedrorum* (Witmer 1996). Data gathered in this study do not allow to evaluate the effect of nutrient concentration of foods taken by frugivores on seed germination. The differences observed in the germination patterns of *Ribes* and *Vaccinium* passed by wild and captive brown bears might well reflect differences in the digestive tracts and diets between them; the possibility exists, however, that such differences are mostly due to the different seed provenances (Chichagof or Juneau).

For a given plant, the outcome of gut treament may also vary with the species of consumer disperser (e.g. Lieberman and Lieberman 1986, Barnea et al. 1990, 1991, 1992, Izhaki and Safriel 1990, Murphy et al. 1993, Mandujano et al. 1994). A different seed retention time, like that between birds (15–45 min) and bears (from several hours to one day, pers. obs.) might be expected to translate into differences in seed coat treatment, and thus in germination. Long retention times can cause the digestion of a large fraction of seeds, as found by Janzen (1982) for horses (which can retain seeds in their guts up to 2 months). In our study, however, no significant differences were observed between the two groups of vertebrates for any of the species studied. Consumer effects were found only in *Sambucus*, but cannot be attributed to differences in gut passage times as seeds ingested by robins behaved similarly to those ingested by bears. Other studies that have compared the effect on germination of different groups of vertebrates have sometimes (Mandujano et al. 1994), but not always (Lieberman and Lieberman 1986), found significant differences between them.

Nevertheless, even if the effect of gut passage on seed germination behaviour is similar between bears and birds, the effect on establishment success is probably quite different, because the number and density of seeds in the scats differ enormously (see Barnea et al. 1992). The large number of seeds in bear scats attracts seed predators (mainly rodents; Bermejo, Traveset and Willson unpubl.), and after germination, seedlings probably

either provide relatively long-term nutrient supplements for surviving seedlings (Bermejo, Traveset, and Willson unpubl.) or facilitate pathogen attack, a detriment to seedlings.

The removal of pulp around the seed may sometimes be sufficient to enhance germination, due to the removal of germination inhibitors in it (Evenari 1949, Mayer and Poljokoff-Mayber 1975, Izhaki and Safriel 1990, Barnea et al. 1991, Witmer and Cheke 1991) or to the reduction of microbial or fungal attack (Ng 1983, Jackson et al. 1988). Although we did not test the effect of pulp on germination, we observed that uneaten mature fruits of *Rubus* and *Streptopus* were rapidly attacked by fungi, both on the plant and on the ground.

No significant differences were found in the germination patterns of the two colour morphs of *Rubus* in this study, or in a parallel study of seed treatment by fruit-eating banana slugs (*Ariolimax columbianus*) (Gervais, Traveset and Willson unpubl.). This suggests that seed dispersers do not have an important selective effect contributing to the maintenance of the colour polymorphism (Traveset and Willson 1997), at least through the mechanism of a differential effect on germination. Such potential selective effect has been reported at least for one species (*Rhagodia parabolica*) (Willson and O'Dowd 1989).

The advantages, if any, of enhanced germination of *Rubus* and *Sambucus* after passing through the dispersers' guts are not clear. One possible implication of an early germination might be, for instance, the reduction of seed predation (Schupp 1993). Early germination might also permit a greater seedling survival, as such seedlings will have attained a greater size (and probably will be more resistant) before the cold winter comes. Germination enhacement has been understood as adaptive in arid ecosystems where rain is unpredictable (Izhaki and Safriel 1990, Izhaki et al. 1995), but such an explanation is probably not relevant in temperate rainforests.

The results obtained in this study support the idea that the advantages of animal seed dispersal may lie more in seed movement away from the parent plant and to specific sites suitable for germination and growth than in seed treatment within dispersers' guts.

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