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The understory vegetation of the Eurasian boreal forest is dominated by several ericaceous species (e.g. bilberry *Vaccinium myrtillus*). These species invest large amounts of energy in their sexual reproduction by producing seed-containing berries, which are apparent adaptations for endozoochory. Their seedlings are, however, almost never found in the wild, and they reproduce virtually exclusively through clones. Brown bears *Ursus arctos* consume enormous amounts of ericaceous berries (predominantly bilberry in central Scandinavia) during hyperphagia, and may facilitate sexual reproduction in such species. If ericaceous species would benefit from endozoochory by brown bears, one would predict that endozoochory would have no negative impacts on germination. We experimentally evaluated this prediction using germination trials under controlled conditions of bilberry seeds that were 1) extracted from brown bear feces, 2) extracted from ripe berries and 3) contained in berries. Using time-to-event analyses, we showed that passing the gut by itself did not stimulate or limit germination. However, seeds that were released from the berries germinated about one month earlier compared to seeds contained in berries. This implies that being released from a fruit, for example through endozoochory, can have a large temporal germination and growth advantage, especially in northern ecosystems a with short growing season.

Keywords: bilberry, brown bear, endozoochory, germination, time-to-event analyses, *Ursus arctos*, *Vaccinium myrtillus*

The understory vegetation of the Eurasian boreal forest is dominated by ericaceous species, such as bilberry *Vaccinium myrtillus*, lingonberry *V. vitis-idaeas* and crowberry *Empetrum nigrum* (Nilsson and Wardle 2005). Each year, these species invest large amounts of energy in the production of seed-containing fruiting bodies (berries), which are apparent adaptations for endozoochory (i.e. seed dispersal after ingestion by animals) (Howe and Smallwood 1982). Yet, their seedlings are rarely found in the wild, and reproduction occurs mostly through clones. This apparent mismatch in energetic investment in sexual reproduction and the rarity of recruitment through seedlings has confused researchers for decades (Kloet and Hill 1994, Eriksson and Fröborg 1996, Welch et al. 2000).

Brown bears *Ursus arctos* in central Scandinavia feed almost exclusively on the berries of Ericaceae, especially bilberry, during autumn (Stenset et al. 2016). Berries are a key food resource in the annual diet of bears, because they are crucial for accumulating fat reserves for winter hibernation.

Annual fluctuations in berry crop production are reflected in the bears' reproductive success, which means that berries exert bottom–up regulatory effects on bears (Hertel et al. 2018). It is therefore not surprising that variation in bilberry production across the landscape affects the spatiotemporal movement behavior of bears (Lodberg-Holm et al. 2019). Bears are important seed dispersers for various plant species, and disperse mostly seeds of fleshy fruit (Gende and Willson 2001, Nowak and Crone 2012, Harrer and Levi 2018). Considering the importance of bilberry in the bears' diet, bears have great potential to function as endozoochorous dispersal vectors for bilberry (Lalleroni et al. 2017).

Dispersal through endozoochory can be beneficial for plant species in many ways. Endozoochory typically promotes long-distance dispersal, which can be important for escaping parental competition and herbivory (Janzen 1970), (re)colonizing habitat (Clark et al. 1998), metapopulation dynamics (Nathan et al. 2008), and bio- and genetic diversity on the landscape scale (Jordano and Godoy 2002, Steyaert et al. 2018). The fecal envelope around seeds dispersed through endozoochory can promote seedling growth and establishment (Traveset et al. 2001), and dispersal agents can direct endozoochory towards ideal germination and establishment (micro)habitat (Wenny and Levey 1998, Steyaert et al. 2018).

To what extent seeds can survive passing the digestive tract of an animal is not unambiguous, and varies between plant species and seed traits, and dispersal vectors, their digestive system, and diet, among others. For example, small and long-lived seeds appear to germinate better after passing the digestive tract of herbivorous and omnivorous dispersers compared to larger or short-lived seeds (Pakeman et al. 2002, Picard et al. 2016). Mechanical (e.g. mastication) or chemical (digestive fluids) scarification of seeds may enhance germination in some species, whereas it can limit survival in others. Seeds typically survive the digestive tract of frugivores, whereas only few would survive that of granivores (Sallabanks and Courtney 1992). The ingestion process in itself may also affect germination by releasing seeds from fruit pulp, which can inhibit germination in several ways (Traveset et al. 2007).

If a mutualistic relationship between brown bears and bilberry would have evolved, in which brown bears benefit from bilberries as a food resource, and bilberries benefit from bears through endozoochory, one would expect that ingestion of seeds and berries does not have a negative impact on germination. Here, we test this hypothesis, by estimating and comparing germination curves (i.e. proportions of germinated seeds over time) of 1) bilberry seeds extracted from brown bears scats, 2) bilberry seeds extracted from berries and 3) seed germination from intact berries (Samuels and Levey 2005). We controlled for two factors that may impact seed germination in bilberry, i.e. the stratification regime, as some ericaceous species require a cold or frost period to trigger germination (Baskin et al. 2000), and the spatial origin of the collected seeds and berries.

Methods

Study system

We conducted our study in a boreal forest ecosystem in the Dalarna and Gävleborg counties in southcentral Sweden (61°N, 14°E). The area has a cool continental climate, with snow cover typically lasting from November to mid-April – early May, and January being the coldest month with average temperatures around −7°C. Mean precipitation during the vegetation period ranges between 350 and 450 mm (Frank et al. 2015). The forest is managed for timber production, with Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* as the commercially most interesting species. Bilberry and other ericaceous species (e.g. lingonberry) dominate the forest floor (Kardell 1979, Hertel et al. 2016). The area harbors a dense population of brown bears, which is monitored by the Scandinavian Brown Bear Research Project. Other potential dispersers of ericaceous species, such as red fox *Vulpes vulpes*, pine marten *Martes martes*, several corvids (*Corvus* spp.) and thrushes (*Turdus* spp.) (Schaumann and Heinken 2002, Harrer and Levi 2018, Steyaert et al. 2018), are common in the study area. The project annually captures about 40–60 bears and marks them with GPS collars, following a standardized protocol, which has been approved by the appropriate management agencies and ethical committees (Djuretiska nämden i Uppsala, Sweden) (Arnemo et al. 2011). The collars are programed to record at

least one GPS location per hour. Refer to (Hertel et al. 2016) for details on the study area and GPS collar specifics.

Data collection

Brown bears typically defecate within the immediate vicinity of their resting sites ('bear beds') (Steyaert et al. 2012). We defined a bear bed as a small-scale disturbance (~1–2 m²) in soil and vegetation and with evidence of bear presence (e.g. bear hair, scats), located in an area where the bear's GPS relocations clustered for at least 4 h within a range of 50 m, and with maximum 30 m between subsequent fixes. For five GPS-marked bears, we collected one fresh scat (<3 days old) at a bear bed during the first week of August 2016. For each focal brown bear, we backtracked its GPS relocations prior to bedding, for collecting bilberry fruits in habitats where the bear had foraged. The gut retention time for a berry diet in Scandinavian brown bears typically ranges between 3 and 16 h (Elfström et al. 2013). Hence, seeds in the collected scat most likely originate from the bear's movement trajectory up to 16 h before bedding. We collected berries at the first backtracked GPS point we encountered with clear signs of bilberry foraging (i.e. shrubs stripped from berries and leaves, berries laying on the forest floor). Pairing seed and scat collection with a 'site ID' allowed us to test and control for spatial dependencies in germination success. We exposed scats and berries to two stratification regimes to account for potential effects of winter temperature on seed germination (Baskin and Baskin 1998). We exposed one portion to a treatment of two weeks at 3°C – 10 weeks at −4°C – 2 weeks at 3°C (frost stratification) (Steyaert et al. 2009), whereas we kept the other batch constant at 3°C during the entire stratification period (cold stratification).

After temperature stratification, we extracted seeds from scat and fruit samples by gently squeezing and dissolving scats or fruit pulp in a water-holding container. Bilberry seeds sink rapidly and are easily separated and collected from other scat and fruit pulp material through centrifuging and pipetting. The centrifugation also randomizes seeds extracted from scats or berries. We rinsed extracted seeds with water and dried them on paper tissue. From the seeds extracted from scats, we used an optical stereo microscope to ensure that all selected seeds for the germination experiment were bilberry seeds.

We randomly selected 10 seeds that were extracted from each scat or fruit sample (n = 200, five site/bear ID × two stratifications × two seed treatments × 10 replications per treatment) and 10 intact fruits per treatment (n = 100). We deposited each seed or intact fruit on 5 g dried and sterilized potting soil on top of a 3–4 cm thick layer of sterilized river sand in a 4 × 4 × 5 cm pot. All pots were randomly distributed on tables in a growth chamber with controlled conditions; i.e. a 12-h day/night light regime, and fixed temperature (22°C) and air humidity (70%) (Steyaert et al. 2009). We monitored each seed and fruit on a daily basis and registered the date of germination for each individual seed when we detected its embryo breaking through the seed coat. As intact bilberries can contain several dozen seeds (often >100) (Ritchie 1956, Ranwala and Naylor 2004), we registered the date of germination of the first seed per

Table 1. Germination curve parameters for bilberry seeds ingested by Scandinavian brown bears ('Ingested'), extracted from fruits ('Extracted'), and seedling emergence from entire fruits ('Fruit'). The parameter 'b' indicates the slope of the curve, parameter 'd' indicates the estimated proportion of germinated seeds/seedling emergence from entire fruits, and 't_{50}' represents the time after sowing at which half of the emerged seedlings appeared. Figures within parentheses indicate the 95% lower and upper confidence limits.

	Germination curve parameter		
Seed treatment	b	d	t_{50}
Ingested	−5.379 (−6.451, −4.307)	0.660 (0.567, 0.753)	21.279 (19.599, 22.959)
Extracted	−5.141 (−6.180, −4.101)	0.660 (0.567, 0.753)	21.594 (19.838, 23.350)
Fruit	−5.438 (−6.665, −4.212)	0.716 (0.623, 0.810)	61.220 (56.568, 65.871)

berry. We started the germination trial on 21 October 2016, and terminated the experiment when germination curves reached their asymptotes.

Data analyses

We assessed potential effects of seed ingestion treatment (ingested, extracted from fruit, seed in fruit), stratification type (cold versus frost stratification), and site/bear ID (five sites) on germination with time-to-event analyses. This statistical technique is commonly applied in seed germination studies when individual seeds are regularly monitored for germination during a specific and discretized (here daily) periods of time (Ritz et al. 2013). As usually not all seeds germinate in a germination experiment, germination data is typically right-censored (i.e. truncated) after a specific period.

We used a cumulative three-parameter log-logistic model function F to fit the proportion of germinated seeds at time t (Ritz et al. 2013) (Eq. 1). The model estimates three parameters. The upper limit parameter d, which denotes the proportion of seeds that germinated at the end of the experiment. The parameter t_{50} represents the time at which 50% of all the seeds that germinated during the trial have germinated, and resembles the median germination time (Ritz et al. 2013). The parameter b is proportional to the

slope at $F(t_{50})$. The model is implemented in the 'drc' package (Ritz et al. 2013) for the R software environment (<www.r-project.org>).

$$F(t) = \frac{d}{1 + \exp\left[b\left\{\log(t) - \log(t_{50})\right\}\right]} \quad (1)$$

The model allows fitting separate curves for explanatory categorical variables, for which their parameter estimates (b, d, t_{50}) can be compared with approximate t-tests. We constructed one separate model for each explanatory variable (seed treatment – ingestion, fruit extracted, entire fruit; stratification – frost versus cold; site/bear ID – five bears/sites) and a null model, and assessed model parsimony among the four candidates using the Akaike information criterion (AIC) and its difference values (ΔAIC) (Akaike 1973, Ritz et al. 2013). We visually assessed model fit by comparing the germination data with the predicted model fits.

Results

We terminated the germination experiment 122 days after sowing. The model with seed ingestion treatment (ΔAIC = 0) outperformed the three other candidates (ΔAIC values >223.8). Germination curves for seeds ingested by bears and seeds extracted from berries were almost identical. Both curves had an estimated proportion of seeds (parameter d) of 0.66 that germinated when we terminated the germination experiment, a median germination time (parameter t_{50}) of about 21 days, and a proportional slope at t_{50} (parameter b, −5.379 and −5.141, respectively) (Table 1, 2, Fig. 1). The germination curve for seeds contained in berries had similar estimates for the slope of the germination curve (−5.438), but had a significantly longer median germination time (about 61 days) or 40 days longer than ingested seeds ($|\beta| = 39.941$, SE = 2.523, p < 0.001) and seeds extracted from fruits ($|\beta| = 39.626$, SE = 2.537, p < 0.001) (Table 1, 2). The estimated proportion of berries from which seedlings emerged was 0.716 (Table 1). The model predictions fitted the germination data very well (Fig. 1). Stratification type

Table 2. Pairwise comparisons (approximate t-test) of the slope (b), proportion (d) and median germination time (t_{50}) according to bilberry seed treatment (bear-ingested 'Ingested', fruit-extracted 'Extracted' and entire fruit 'Fruit'), stratification type (Cold versus Frost) and bearID/site.

|	b			d			t_{50}		
Pairwise comparison	β	SE	p	β	SE	p	β	SE	p
Ingested versus Fruit	−0.056	0.067	0.401	0.060	0.831	0.943	−39.941	2.523	<0.001
Ingested versus Extracted	0.000	0.067	1.000	−0.238	0.762	0.755	−0.315	1.240	0.799
Fruit versus Extracted	0.056	0.067	0.401	−0.298	0.820	0.717	39.626	2.537	<0.001
Cold versus Frost stratification	0.074	0.056	0.187	0.303	0.360	0.400	−0.634	2.990	0.832
Radika versus Salga	0.091	0.086	0.295	0.359	0.563	0.524	−0.666	4.192	0.874
Radika versus Lutane	0.104	0.087	0.232	0.374	0.574	0.515	−4.017	4.445	0.366
Radika versus Grivla	0.049	0.086	0.568	0.270	0.559	0.629	−5.490	4.599	0.233
Radika versus Bergsloga	0.054	0.089	0.543	−0.270	0.522	0.605	−3.368	5.198	0.517
Salga versus Lutane	0.014	0.090	0.879	0.015	0.607	0.981	−3.351	4.338	0.440
Salga versus Grivla	−0.041	0.089	0.641	−0.089	0.593	0.881	−4.825	4.495	0.283
Salga versus Bergsloga	−0.036	0.091	0.690	−0.629	0.558	0.260	−2.702	5.107	0.597
Lutane versus Grivla	−0.055	0.090	0.539	−0.104	0.603	0.864	−1.474	4.732	0.756
Lutane versus Bergsloga	−0.050	0.092	0.587	−0.644	0.570	0.259	0.649	5.316	0.903
Grivla versus Bergsloga	0.005	0.091	0.957	−0.540	0.554	0.330	2.122	5.446	0.697

3
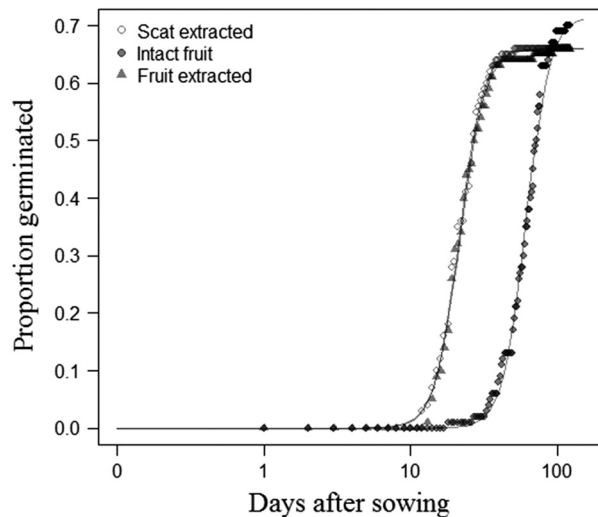
Figure 1. Germination curves of bilberry seeds that were ingested by Scandinavian brown bears (open dots) or extracted from fruits (triangles), and for seedling emergence from intact fruits (fill dots), according to the most supported three-parameter dose–response-model to assess germination in bilberry.

and Site/bear ID did not significantly affect germination curve parameters (Table 2).

Discussion

The key finding of our study is that the germination likelihood of bilberry seeds does not seem to be affected by passing the digestive tract of brown bears. When encapsulated in berries, however, germination was delayed by more than one month. The mechanism causing this germination inhibition (e.g. light deficiency for incapsulated seeds, secondary metabolites or osmotic pressure from sugar-rich pulp) (Traveset et al. 2007) remains, however, unclear. We found that bilberry seeds could germinate without a cold or frost stratification, indicating that seeds can germinate immediately after being released from the fruit. This implies that endozoochory by brown bears can advance germination and establishment for bilberry. Our findings are in line with a study from Nowak and Crone (2012). These authors documented similar germination rates for seeds extracted from fruits and seeds ingested by brown and American black bears *U. americanus* for several fleshy fruits (including huckleberries, *Vaccinium* spp.), but much lower germination rates for seeds contained in fruits during their four-week germination experiment. Traveset and Wilson (1997) also documented similar germination rates for bear-ingested and uningested seeds of various fleshy fruits in an Alaskan study system. McKonkey and Galetti (1999) reported similar germination rates of uningested *Canarium* seeds and those ingested by sun bears *Helarctos malayanus* in a tropical forest in central Borneo. Note, however, that our results are derived from a controlled experiment, in which seeds were cleaned from fecal material or pulp, which under natural conditions could reduce germination potential, because of, for example, microbial activity of germination inhibitors in pulp (Traveset et al. 2007).

The advantages for bilberry being dispersed through endozoochory by bears probably relate to other mechanisms than germination enhancement through passing the digestive tract (Traveset and Willson 1997). For example, brown bears in Scandinavia have large home ranges (up to several 100 km²) (Hertel et al. 2019) and can cover large distances in limited time (several kilometers within a 16-h gut retention time) (Martin et al. 2013). This implies that brown bears can disperse plant seed over long distances (Willson and Gende 2004, Lalleroni et al. 2017). Long-distance dispersal through endozoochory has also been documented in other bear species (e.g. Asiatic black bear *Ursus thibetanus*) and ecosystems (Takahashi et al. 2008, Koike et al. 2011), and even allows certain plant species (e.g. cherry species *Prunus* spp.) to keep ahead of climate change (Naoe et al. 2016). Long-distance dispersal of plant seed is an important mechanism for plants to escape parental competition, (re)colonize habitat and maintain metapopulation dynamics and genetic diversity at the landscape scale (Howe and Smallwood 1982, Howe 1986, Nathan et al. 2008). In addition, bears often defecate into or in the immediate vicinity of their resting sites (Steyaert et al. 2012), which typically resemble small-scale disturbances in the vegetation and soil (Craighead et al. 1995). Previous studies indicated that such disturbances are crucial for the establishment of bilberry from seed (Eriksson and Fröborg 1996). Hence, bears may not only disperse viable bilberry seeds, they may also generate ideal germination and establishment conditions for seeds, and direct dispersal towards those sites. This would imply that bears facilitate sexual reproduction of bilberry and perhaps other species with similar dispersal characteristics, and may facilitate sexual reproduction in berry producing species with predominant clonal propagation. However, this idea remains to be tested. Another potential benefit for being dispersed through endozoochory by bears (and perhaps other animals), is that the seeds are contained in a fecal envelope, that can support germination, seedling growth and eventual establishment. The potential costs (e.g. seedling competition in fecal depositions) and benefits of endozoochory for dispersal in bilberry remain, however, to be tested.

Brown bears share their habitat with several other mammals and birds that consume berries of ericaceous species, which may be important dispersal agents for these species as well. The relative contribution of various potential dispersers to endozoochorous dispersal and sexual reproduction of ericaceous species in northern ecosystems remains largely unexplored (but see Harrer and Levi 2018), and warrants future attention.

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