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Abstract

Arctic foxes are evaluated as seed dispersal vectors for Greenlandic plant species through a feeding experiment with subsequent scat analysis and germination test. Seeds of 22 common species with different morphology were tested. Passage time ranged between 4 and 48 h. No significant differences were detected in passage time for seeds with different morphology. *Cerastium alpinum* and *Stellaria longipes* had higher germination after passage through the fox's digestive tract when compared to controls. *Sibbaldia procumbens*, *Oxyria digyna*, and *Silene acaulis* were favored by passage when shorter than 10 h. *Salix glauca* ssp. *callicarpaea*, *Veronica alpina*, *Gnaphalium norvegicum*, *Papaver radicatum*, *Ranunculus hyperboreus*, *Chamaenerion latifolium*, *Luzula parviflora*, and bulbils of *Polygonum viviparum* and *Saxifraga cernua* were inhibited by passage, whereas the remaining species had germination percentage too low to allow for evaluation. Species with adaptations to wind dispersal seemed particularly vulnerable to gut passage. Arctic foxes are able to provide long-distance dispersal of seeds lacking morphological adaptations to dispersal, but for most species seeds need to be defecated within 12 h to remain viable.

Introduction

During the early Holocene there was a rapid migration of plants and animals toward the newly deglaciated regions in the north. Seed dispersal must have been very efficient and long ranging, yet the rapid migration is poorly explained by our present knowledge of dispersal. Clark et al. (1998) argued that occasional long-distance seed dispersal events must have been very important in recolonization after glaciation.

Similarly, most plant species in Greenland have spread thousands of kilometers during the first couple of millennia of the Holocene to reach their current distribution, and in steps to hundreds of kilometers to pass over the sea (Iversen, 1954; Fredskild, 1973, 1996; Funder, 1989; Bennike, 1999). Seeds of most arctic plant species are small and often have adaptations for wind dispersal, and Porsild (1910) suggested that most species were dispersed over long distances by wind. However, wind dispersal over long distances may cause enormous losses of seeds, particularly where dispersal routes cross great distances of water or ice. Warming (1887), Iversen (1954), and Bennike (1999) suggested that chance dispersal by birds is important, but other animals have not been considered, and so far no experiments have been conducted to identify seed dispersal vectors in Greenland.

Clark et al. (1998) described frugivorous mammals, such as foxes and bears, as underappreciated agents of long-distance seed dispersal. Canids have been shown to act as seed dispersal agents of native plant species in many ecosystems, e.g. tropical savanna grasslands (Motta-Junior et al., 1994; Motta-Junior and Martins, 2002), mediterranean shrublands (Bustamante et al., 1992; Castro et al., 1994; Leon Lobos and Kalin Arroyo, 1994; Aronne and Russo, 1997; Wilson and Thomas, 1999), temperate grasslands (Jaeger, 1950; Cypher and Cypher, 1999), and boreal forest and tundra (Willson, 1993), as well as of invasive species (Brunner et al., 1976; Meek, 1998). Almost all of these studies have focused on frugivory, and seed dispersal of fleshy-fruited species by carnivores has been an area of focus recently (Traveset, 1998; Traveset and Verdú, 2002).

The arctic fox (*Alopex lagopus*) is known to consume fleshy fruits (Birks and Penford, 1990; Nielsen, 1994; Frafjord, 1995; Kapel, 1999). Only a few arctic plant species develop fleshy fruits, but other seed types may be consumed unintentionally with prey items handled on the ground or buried in caches, because soil would be ingested in these processes. Alternatively, they may originate from the guts of prey items, namely indirect or secondary seed dispersal, a phenomenon shown for carnivorous birds (Darwin, 1859; Dean and Milton, 1988; Nogales et al., 1998, 2002) and feral cats (Nogales et al., 1996). Berries and vegetative plant parts, as well as soil, have been frequently reported from arctic fox scats and stomach samples (e.g., Garrott et al., 1983; Prestrud, 1992; Hersteinsson and Macdonald, 1996; Kapel, 1999; Elmhagen et al., 2000), and though we do not have data on the actual seed and bulbil content in fox scats yet, it is very likely that seeds and bulbils (henceforth both called seeds) are unintentionally eaten by foxes from time to time and that foxes can provide rare but long-distance seed dispersal events for species without morphological adaptations to endozoochory.

The summer home range of arctic foxes is in the magnitude of 20 to 60 km^2, but varies between locations and years (Angerbjörn et al., 1997; Zakrzewski et al., 1999). Arctic foxes have been recorded to occasionally move between 800 and 2000 km during the period from October to May (Braestrup, 1941; Wrigley and Hatch, 1976; Eberhardt et al., 1983; Bennike, 1999). This implies minimum mean daily movements of up to 10 km, and potentially much farther.

Depending on the gut passage time, the animal may disperse seeds over long distances to new suitable sites. Arctic foxes' gut retention time seems to be relatively short compared to that of seeds observed in animals of comparable sizes (Hickey et al., 1999; Williams et al., 2000). Szuman and Skrzydlewski (1962) found the defecation patterns of caged arctic foxes to be highly variable. In general, the first defecation after a meal took place after a minimum of 3 to 4 h, but normally after 9 h, and the last defecation took place within 27 h. However, after complete gut evacuation, particles might rest in the

TABLE 1

Number of seeds recovered in the scats and recover percentage of total given for the studied species. Seed morphology is given and the mean passage time with std dev. for each species

	n	Recovery percentage	Seed morphology	Mean passage time	Std dev.
Saxifraga cernua	103	52	bulbil	16.19	7.00
Bartsia alpina	278	56	flat	18.10	8.83
Polygonum viviparum	403	81	bulbil	18.74	9.32
Chamaenerion latifolium	107	54	app.	18.99	8.04
Oxyria digyna	170	85	flat	19.08	8.57
Cerastium alpinum	380	76	unsp.	19.43	8.83
Ranunculus hyperboreus	110	73	unsp.	19.64	8.54
Salix glauca ssp callicarpaea	222	44	app.	19.71	9.64
Saxifraga tricuspidata	243	49	unsp.	20.10	10.06
Pedicularis hirsuta	441	88	unsp.	20.21	9.46
Betula nana	190	76	flat	20.44	10.01
Luzula parviflora	151	76	unsp.	21.11	9.18
Gnaphalium norvegicum	111	22	app.	21.23	9.18
Sibbaldia procumbens	318	80	unsp.	21.35	10.24
Veronica alpina	175	35	unsp.	21.42	9.54
Silene acaulis	119	60	unsp.	21.65	10.85
Stellaria longipes	421	84	unsp.	21.81	9.69
Papaver radicatum	387	77	unsp.	21.98	10.25
Vaccinium uliginosum	367	41	berry	22.37	9.19
Dryas integrifolia	399	80	app.	23.46	10.03
Erjophorum scheuchzeri	86	86	app.	25.12	10.51
Empetrum nigrum	241	54	berry	25.48	10.58

appendix. Seeds may therefore be dispersed over at least 10 km if they stay in the gut for 24 h, and even by staying just 9 h within the animal, a fox may often have moved several kilometers.

Passage of seeds through animal digestive tracts may enhance or inhibit germination. In a meta-analysis, Traveset (1998) found that 8 out of 28 studies showed germination to be significantly enhanced, the rest finding no significant effect. Traveset and Willson (1997) reported that most species showed enhancement, many showed no significant effect, and fewer studies observed species to envisage considerable losses in germinability during passage. For canids, studies by Cypher and Cypher (1999), Motta-Junior and Martins (2002), and Traveset et al. (2001) have found some plant species to suffer considerable losses during gut passage.

In this study, we experimentally fed arctic foxes with seeds from both fleshy- and nonfleshy-fruited plant species from Greenland to investigate (a) the passage time, once ingested, of seeds through the digestive tract of the fox, and (b) how passage through the fox affects the germination ability of the plant species.

Methods

Diaspores of 21 species and bulbils of 2 species (Table 1) were collected on Disko, Western Greenland, in August, September, and October 2001. The species were selected for seeds with as much different morphology and size as we could find. However, the species with the smallest seeds, *Cassiope tetragona*, was excluded from the experiment because of difficulties with handling it. The seeds were dried and stored at room temperature until the feeding experiment, except for berries of *Vaccinium uliginosum* and *Empetrum nigrum* ssp. *hermaphroditum*, which were kept frozen until the experiment. In the feeding experiment, the seeds were given within intact berries, and seed number per berry was calculated by dissecting 20 berries of each species and counting number of seeds within them to calculate an average number per species. For

TABLE 2

Mean passage time and std dev. for the species categorized after morphological adaptations to seed dispersal

Bulbils	18.22	8.95
Flat	19.07	9.15
Unspecialized	20.89	9.72
Append.	21.90	9.88
Fleshy	23.60	9.88

convenience, seeds of the two fleshy-fruited species, bulbils of two species, and diaspores (including achenes and similar seeds) of the remaining 18 species are henceforth all called seeds. Species will be identified by their generic names in the following, except *Saxifraga tricuspidata* and *S. cernua*. Nomenclature follows Böcher et al. (1978).

Ten arctic foxes (three males and seven females) kept at the Royal Agricultural University in Copenhagen were included in the experiment. The foxes were held in separate standard farm cages ($0.8 \times 1.2 \times 0.95$ m) with the net bottom elevated about 1 m above the ground. A wooden tray beneath each cage collected the scats from each fox separately, while letting the urine run off. Foxes were fed on a dog plate within the cage once a day in the late afternoon. Leftovers from the meal, such as pieces of meat or bones that had fallen through the net bottom, were put back on the plate in the cage after each collection event.

To simulate a natural diet in Greenland (Nielsen, 1991), the foxes were fed daily 125 g of poultry (newly hatched but dead chicken) and 125 g of mixed raw fish (cod, *Gadus morhua*; herring, *Culpea harengus*; flounder, *Platichthys flesus*; and whiting, *Merlangius merlangius*). All parts of the chickens and fish were included. After 72 h on this diet, seeds were mixed into some raw liver and given before a meal. All the liver with seeds was consumed readily, and in general the foxes ate all the food they were given during the experiment. After the meal containing seeds, scats were collected every 4 h during the following 52 h.

The scats were washed through a 250 μm sieve. The resulting samples were analyzed under a dissecting microscope. Seeds were counted and put in Petri dishes lined with moist filter paper for subsequent germination. The procedure involved soaking the seeds in water in the Petri dishes for about 24 h at room temperature, followed by 24 h in a refrigerator. Thereafter, the seeds were kept on wet filter paper at room temperature (18–23°C) in a southeast-facing window for 8 weeks. Three controls were made for each species with seeds that had not passed through the fox guts, but which had otherwise been treated similarly. Number of seeds in the controls varied due to shortage of seeds from some species (see Table 3). Germination in the controls was noted after 2, 3, 4, 5, 6, and 7 weeks.

Germination of the seeds (radicle or shoot emergence) was noted for each species at each sampling time after 3, 5, 7 and 8 weeks until there was no further germination for any species since last recording. After 3 weeks all the seeds infected with fungi were removed from the dishes.

Differences in means in passage time were analyzed with a Z-test. Differences between germination percentage in scats and controls was analyzed by a Chi square test with Yates correction, and correlations between passage-time and germination percentages were calculated with Spearman Rank correlation after excluding passage times with less than 5 seeds (Fowler and Cohen 1990).

Results

For most species the percentage of seeds recovered was relatively high (Table 1): 11 of the 22 species had percentages of more than 75%, 6 species had percentages between 50% and 75%, and only *Gnaphalium* and *Veronica* had percentages lower than 40%. The mean passage time
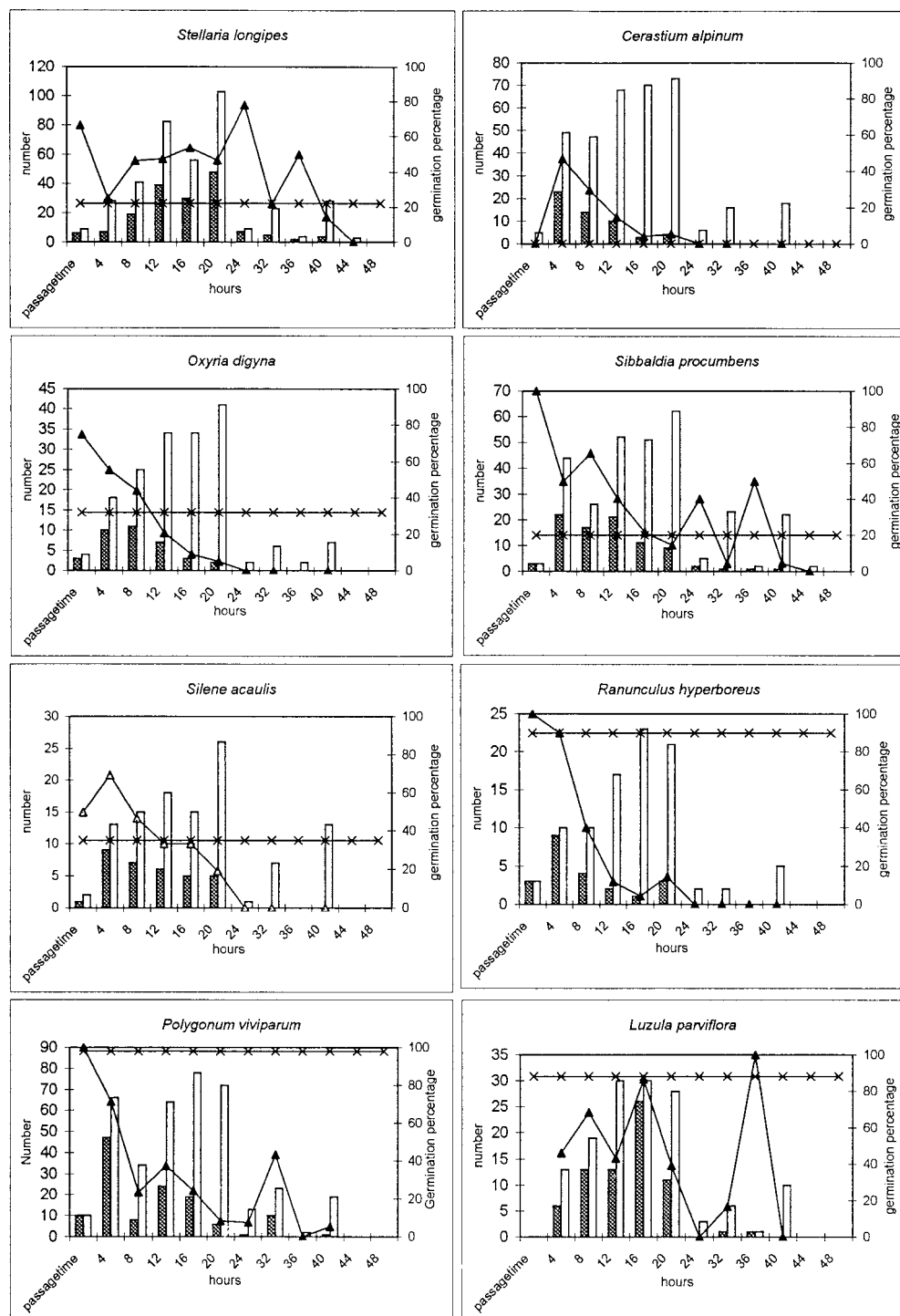
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FIGURE 1. *Germination percentages for the 8 most efficiently germinating species in the experiment. Horizontal curve (-✕-) gives germination percent for control. The other curve (-▲-) gives germination percentage for scats collected at the given passage time. The bars give number of seeds passed in scats at that passage time (white bars), and number of these seeds that germinated (dark bars).*

of the seeds varied between 16.2 and 25.5 h for the individual species, but the standard deviation was quite high, indicating a considerable variation in passage time within species. Some foxes passed many seeds after 4 h, whereas others did not produce any scats with seeds until after 20 h. After 44 h there were still seeds of all species in the scats except for *Saxifraga cernua*, which had its last bulbil recovered in a scat after 40 h. Eighteen seeds of 12 different species were found after 48 h but none after 52 h.

The fleshy-fruited species and the species with appendages had the longest mean passage time, but due to the large intraspecific variation the differences in mean passage time were not statistically different, neither between individual species nor between groups of species with different morphology (Table 2).

In Figure 1, the average germination percentage over time is shown together with the average germination percentage in the three controls (with curves). The bars show number of seeds found at each time (for the seeds that appeared unaffected by fungi after 3 weeks) together with the number of germinated seeds. Only the 8 species with more than 20 germinated seeds each in the scats are included in the

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TABLE 3

Number of seeds in germination samples and germination percentages as means of the three controls and of all samples collected from the scats (unaffected by fungy after three weeks, see text)

	Number of seeds in each of 3 controls	Germination percentage controls	Total number of seeds from scats	Germination percentage scats	Diff. Between germination percentages
Inhibited by treatment					
Saxifraga cernua	20	92	95	0	p < 0.001
Salix glauca ssp callicarpaea	20	80	201	0	p < 0.001
Veronica alpina	20	92	162	5	p < 0.001
Gnaphalium norvegicum	20	53	103	0	p < 0.001
Papaver radicatum	20	53	360	1	p < 0.001
Ranunculus hyperboreus	20	90	93	24	p < 0.001
Polygonum viviparum	20	98	381	33	p < 0.001
Chamaenerion latifolium	20	37	94	3	p < 0.001
Luzula parviflora	20	88	140	51	p < 0.001
Favored by treatment					
Cerastium alpinum	20	0	352	15	p < 0.001
Stellaria longipes	20	22	386	43	p < 0.001
No significant difference					
Sibbaldia procumbens	20	20	292	30	ns
Oxyria digyna	20	32	173	21	ns
Silene acaulis	10	35	110	30	ns

figure. Spearman rank correlations between passage time and germination ability is given for each species (passage times with less than 5 seeds are excluded). The chance of germination decreased significantly with passage time for all species except *Stellaria*, *Cerastium*, and *Luzula*, but *Luzula* was marginally significant. For most species, there was no germination after 24 h. The seeds of *Stellaria* were either favored or unaffected when passed within 40 h. The curves show how germination percentages for *Stellaria* and *Cerastium* are higher than controls at any time of passage (*Cerastium* control germination = 0%). *Oxyria*, *Sibbaldia*, and *Silene* seem to be favored by passage when passage time was short (<12–16 h), whereas *Ranunculus*, *Luzula*, and *Polygonum* had lower or equivalent chance of germinating after passage, even when passage time was short. *Luzula* had a peak at 40 h, but this was caused by a single seed, as indicated by the seed and germination columns.

Seeds of 3 species did not germinate at all, neither in the controls nor in the samples recovered from the scats. Five species had small germination percentages (<10%) in both control and after passage. For the remaining 14 species, Table 3 gives average germination percentages in the 3 controls and the germination percentage for all seeds of each of the species in the scats. Nine species had significantly higher germination in the control than in the treatment. The germination of bulbils of *Saxifraga cernua* and of seeds of *Salix*, *Veronica*, *Gnaphalium*, *Papaver*, *and Chamaenerion* had hardly any germination after passage. Two species had higher germination after passage through fox guts as compared to the controls. Germination percentages of *Oxyria*, *Sibbaldia*, and *Silene* were not significantly different but as Figure 1 shows, this is due to the higher germination percentage if passage time was short, whereas the germination percentage decreased drastically for the slow passing seeds.

Discussion

In the present study we have demonstrated that all the investigated species are able to be carried in fox guts for 44–48 h. This passage time is of intermediate length among mammals of comparable body size. It is longer than that reported for berries fed to *Martes americana* (4–5 h; Hickey et al., 1999), but shorter than that reported for opossums (many days; Williams et al. 2000). Szuman and Skrydlewski (1962) reported passage times of entire meals to be 27 h in Arctic foxes. Seeds seem to pass through the digestive tract of the foxes at the same speed as other food items, with no significant differences for different seed morphology. This disagrees with what has been reported by DeVlaming and Proctor (1968) for waterbirds, in which species of Cyperaceae pass slowly, whereas species of Asteraceae rarely retain for more than a few hours.

Slow passage increases the potential dispersal distance, but need not increase the efficiency of the endozoochorous seed disperser. *Sibbaldia*, *Oxyria*, and *Silene* were only favored if passage was fast, and for most species the germination ability decreased with time, meaning that the seeds of most species need to pass within 12–24 h to remain viable. This limits the dispersal distance that the seeds can obtain with the arctic fox as a dispersal vector. However, an arctic fox can run several kilometers within a few hours, and may therefore increase the normal dispersal distances for these species many-fold compared to unassisted dispersal.

Among species favored by the treatment, *Cerastium alpinum* is the most remarkable. No germination experiments have been carried out so far on this species, according to Baskin and Baskin (1998). Immersion in water during germination may increase germination in this species, as is the case for *Cerastium arcticum* (Bell and Bliss, 1980), but passage through the fox also broke the dormancy. *Stellaria* was also favored by passage. This is remarkable, as there are reports from the study region that this species is considerably more abundant around dens of arctic foxes than in the near surroundings (Nielsen et al., 1994). Other Caryophyllaceae, *Cerastium alpinum* and *Stellaria calycantha*, have been found to behave similarly near dens of arctic foxes in Scandinavia (Bruun et al., 2005).

Studies of fleshy-fruited species eaten by foxes have shown germination percentages up to 50–70% (Aronne and Russo 1997; Meek, 1998). However, the 2 species in the present study showed no germination, neither after passage nor in controls. Unfortunately, we did not stratify any of the seeds before the experiment. However, *Betula nana*, *Empetrum nigrum* ssp. *hermaphroditum*, and *Vaccinium uliginosum* have physiological dormancy according to Vander Kloet and Hill (1994), Baskin and Baskin (1998), and Baskin et al. (2000, 2002). Vander Kloet and Hill (2000) showed high germination percentages for *Vaccinium uliginosum* after stratification of seeds in scats as well as seeds cleaned from fruit (59–69%), whereas seeds without stratification only obtained germination percentages of 0–5%. The results for these 3 species, and the other species with little germination therefore have no value with respect to the germination question of this study.

Species with long appendages and *Saxifraga cernua*, *Veronica*, and *Papaver* were strongly inhibited by passage. The seeds of these species all imbibed after passage and seemed to be more infected by fungi than most other species. This may be due to the thin seed coats of these species or, for bulbils of *Saxifraga cernua*, no seed coat. DeVlaming and Proctor (1968) showed that only seeds with hard integuments or small size were able to survive passage through the avian intestinal tract. Species with adaptations to wind dispersal do not have the same need for animals as long-distance dispersal vectors as do others. How long-distance dispersal of *Saxifraga cernua*, *Veronica*, and *Papaver* might take place still remains unclear, but the present study does not support endozoochorous dispersal for these species. *Saxifraga cernua* is widespread and a rapid colonizer in the region (Graae et al.,

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unpublished). *Papaver* is also widespread and a ruderal species, but this may relate to seed bank as well as dispersal (Hansen, 2003). Both these species were probably early immigrants (Fredskild, 1973). *Veronica* is at its northern limit in the region but is widespread in southern Greenland. It arrived late in Greenland (Fredskild, 1973), probably because it needed higher temperatures before it could colonize.

In conclusion, the present study indicates that seeds of many arctic plant species, once ingested, can survive passage through the guts of the arctic fox and thereby become dispersed over considerable distances. This result calls for quantitative fields studies on which species actually become ingested and eventually defecated by arctic foxes, and on the effect upon seed germination and plant recruitment of seeds ending up in fox scats.

Acknowledgments

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