Sheep as endozoochoric seed dispersers in areas of primary succession

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Abstract

Seed dispersal by herbivorous mammal endozoochory can be an efficient means of transport to new habitats, and may be especially important in poorly vegetated sites where there is little existing seed pool. In Iceland, where there are no indigenous large herbivores, the high numbers of freely grazing sheep in poorly vegetated summer grazing lands, may have a significant role as seed dispersers.

To gain insight into the role of endozoochorous dispersal, 16 samples of sheep dung were collected at Skeiðarársandur, a glacial outwash plain in SE-Iceland. Dung samples were collected in August and October 2015 and grown in a greenhouse environment. Results showed that sheep on Skeiðarársandur disperse various species through endozoochory, yet were preferentially selective in the consumption of species dispersed. Sheep dispersed 25.8% of the available species recorded on Skeiðarársandur. Of the 24 dispersed species, 8 species had not yet been identified in the representative vegetation for the area. Species considered rare in abundance on Skeiðarársandur, represented 54 % of dispersed species, supporting the idea sheep are preferentially selective in plant consumption. Contrary to expectations, there was no correlation between proportion of dispersed species and seed mass and plant height. Species with high palatability, expected to disproportionally represent dispersed species, represent 42 % of dispersed species.

Selective dispersal by sheep endozoochory may potentially play a key role in species diversity and richness, especially as it relates to sites of primary succession, where there is only a small and species-poor local seed pool.

Keywords: Endoozoochory, sheep grazing, seed dispersal, primary succession, poorly vegetated, Skeiðarársandur, Iceland, nature protection, plant diversity

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1 Introduction

Seed dispersal is a critical stage in the lifecycle of the plant, ensuring the continued existence of a population (Harper 1977). Although this stage is necessary for continued existence, plants are limited in their means of dispersal (Primack & Miao 1992) and the limitations of seed dispersal strongly influence species local and regional composition, diversity, and population persistence (MacArthur and Wilson 1967, Cornell and Lawton 1992, Eriksson 1993). Dispersal limitation often outweighs abiotic limitations in determining plant establishment (Zobel et al. 2000, Butaye et al. 2002, Tofts and Silvertown 2002), even in areas of primary succession, with generally unfavorable conditions for the establishment of vascular plants (Walker & del Moral 2003). Thus, plants have evolved to rely on dispersal mechanisms such as wind, water, animal-assisted dispersal (endozoochory or epizoochory), or, as commonly found in small-seeded species, unassisted dispersal (Howe & Smallwood 1982). The mechanism(s) in which seeds are dispersed, serve as a type of ecological filter, influencing the distance seeds travel and subsequent plant community characteristics and dynmics.

Endozoochory, animal seed dispersal through ingestion and digestion of seeds or spores, has been shown to be an efficient mechanism for long-distance seed dispersal in various ecosystems. Many studies show that herbivorous mammals are important vectors for seed dispersal (Welch 1985, Malo & Suarez 1995, Fischer et al. 1996, Heinken et al. 2002, Pakeman et al. 2002, Cosyns et al. 2005a,b, Bakker et al. 2008) while large herbivores, such as ungulates, have the greatest impact on seed dispersal (Malo & Suarez 1995). Large mammalian herbivores could potentially be important dispersers of small seeds (< 0.1 mg) that are usually characterized with 'unassisted' means of dispersal (Hughes et al. 1994), with support from the 'foliage is the fruit' hypothesis on the dispersion of dry, inconspicuous seeds as a result of the primary consumption of plant foliage (fruit) (Janzen 1984). As a result of the seed mass to seed number tradeoff, small seeded species would be expected to be over-represented compared to large ones in dispersed individuals (Bruun & Poschlod 2006), as smaller seeds are better able to bypass the grinding motion of consumption and withstand the enzymes and microbes of ungulate digestion (Pakeman et al. 2002).

Depending on the grazer's body size, seed retention via endozoochory can last anywhere from less than one day to several days, allowing long distance seed dispersal to take place (Cosyns et al. 2005b). Ungulates are considered long-distance seed dispersal agents (i.e. greater than 100 m) (Cain et al. 2000), transporting plant species usually across supra-kilometric distances (Fischer et al. 1996, Mouissie et al. 2005a). The role of endozoochory has been studied in grasslands and other well-vegetated sites, but few studies exist on the role of endozoochory in poorly vegetated sites, such as those undergoing primary succession.

In sites of primary succession, where there is little existing seed pool, endozoochory may serve as a critical long-distance seed dispersal mechanism. During the initial stages of succession, seed input comes mostly from long-distance dispersal. After which, a seed bank builds up and local seed production takes over as the most prominent seed source (del

Moral et al. 2005). For many plant species, this initial long-distance dispersal can occur using an animal vector. In areas with little seed pool, the presence or absence of this dispersal mechanism and its role as an ecological filter could significantly influence the species composition and characteristics. In addition, endozoochory may play a key role in plant establishment post-dispersal, especially as it relates to areas of primary succession. Endozoochory dispersal may promote nitrogen cycling through localized urine and feces deposition (Steinauer and Collins 1995, Hobbs 1996). In areas where conditions are harsh and nutrient levels low, this additional fertilizer at the time and site of dispersal may give endozoochorically dispersed species an advantage in establishment. Additionally the activities of grazing sheep create small-scale disturbances (Faust et al. 2011, Rosenthal et al. 2012), providing re-generation niches (Bakker & Olff 2003), assistance incorporating seeds into the soil, (Eichberg et al. 2005, Heinken et al. 2006) and stimulating seed bank germination (Malo et al. 1995). Species dispersed in sheep dung amongst these small-scale disturbances may be provided an environmental advantage, especially so in the harsh conditions found in areas of primary succession,

I studied the role of ungulate endozoochory as a dispersal mechanism in primary succession on Skeiðarársandur, a 1000 km^2 poorly vegetated glacial outwash plain in SE-Iceland. The area of Skeiðarársandur in SE-Iceland is of particular interest due to its variation in vegetation cover and high frequency of sheep grazing. While Skeiðarársandur is primarily sparsely vegetated (75 % of total area), at stages of early primary succession, some parts have developed into continuous moss heathland, with herbs and few small birch and willow shrubs (Kofler 2004). For more than 60 years there has been a history of domesticated sheep grazing in the summer months (from early June until September) by approximately 200 ewes plus lamb (each ewe has two lambs in general) at the sand plain (Búnaðarsamband Suðurlands). These freely grazing sheep are likely to play a critical role in the long-distance dispersal of seeds, as they can retain ingested plant matter for several days and travel kilometric distances. A majority of seeds ingested by sheep are retained for 24-40 hours, although some seeds (<1%) are retained 76 to 160 hours after feeding (Manzano et al. 2006). Likewise, sheep are selective grazers. Arguably, sheep do not consume all available vegetation (Grant 1985), but instead it is assumed they preferentially consume based on plant characteristics. Sheep grazing consumption increases with increased plant height (Allden & McDWhittaker 1970, Díaz et al. 2001) and it is also assumed additional plant and seed characteristics such as seed mass or platability could influence the increased or decreased probability of dispersal by endozoochory (Albert et al. 2015, Bakker et al. 2008, Couvreur et al. 2005, Kuiters & Huiskes 2010, Pakeman et al. 2002). Previous study on Skeiðarársandur underlines the importance of dispersal limitation in plant establishment (Marteinsdóttir et al. 2010), thus seep could be an important dispersal vector for this area.

The main aim of this study is to understand the role and significance of freely grazing sheep as a potential dispersal mechanism in an area of primary succession in Iceland. My research questions were: (1) Based on the representational vegetation in the area, what plant species are being dispersed by sheep endozoochory? (2) Does the amount of seed dispersed by endozoochory change over the season? And (3) do species dispersed by endozoochory have some specific characteristics? Although many researchers have investigated the potential role of ungulates in dispersing seeds, surprisingly few of them have quantitatively compared the dispersed species with the available plant species in a disperser's range (Mouissie et al. 2005b, Albert et al. 2015a, Heinken et al. 2002, Kuiters and Huiskes 2010, Malo & Suárez 1995 and Traba et al. 2003). This comparison is necessary to distinguish plant selection and subsequent plant dispersal simply from plant availability in the study area (Pakeman & Eastwood 2013). Furthermore, fewer of these comparisons incorporated plant traits such as palatability or seed mass, though this approach could offer insight into ecosystem functioning (Bakker et al. 2008, Kuiters & Huiskes 2010, Pakeman et al. 2002). Lastly, no study to my knowledge has examined the role of an ungulate as a mechanism for seed dispersal via endozoochory specifically in areas of primary succession. A basic lack of knowledge of ungulates as potential dispersal mechanisms in primary and early successional sites creates a need to examine the impact of this dispersal mechanism as it relates to primary and early successional plant communities.

I hypothesize the plant species consumed, retained, and dispersed by the grazer are likely to be only a fraction of the total available species in the area. In this role as a long-distance dispersal mechanism, the grazer serves as a significant ecological filter and thus the plant species dispersed via endozoochory are not a random sample drawn from the available species. It is assumed that seed dispersal by this grazing mechanism acts as an ecological filter based on specific species characteristics, such as palatability, plant height, and seed mass. Plants characterized as more palatable and with increasing height are assumed to be preferentially consumed, while a smaller seed mass is likely to better survie ungulate digestion. It is hypothesized that species with a higher consumption preference by sheep (higher palatability), smaller seed mass, and increased plant height will be will be disproportionally over-represented in germinated species from the dung samples. By examining chosen plant and seed characteristics thought to influence dispersal by sheep endozoochory (plant classification, palatability, seed mass, average plant height, and abundance), it is possible to make some generalizations about the dispersed species and sheep grazing preferences. These generalizations can be used to predict the species likely to be dispersed by endozoochory and improve our understanding of endozoochory as a seed dispersal mechanism.

1 Methodology

1.1 Study Site

The observational study examines dung samples collected from sixteen sites at Skeiðarársandur in SE-Iceland. Skeiðarársandur is an outwash plain in front of Skeiðarárjökull, the largest outlet glacier of Vatnajökull icecap, Iceland. This area is a flat, dry and sandy plain with shallow depressions representing previous river pathways . The soil in this area is composed primarily of volcanic glass and is quite infertile, with very low nitrogen and carbon concentrations (Marteinsdóttir et al. 2010, Svavarsdóttir and Þórhallsdóttir, unpublished data). The climate in this area is comprised of cool summers and mild winters with a growing season that lasts from mid-May to early September. The mean summer (June-August) temperature for the area was 9.9 °C (± 0.07) and the mean summer precipitation was 130 mm (± 5.1). The mean annual air temperature was 4.9 °C (± 0.07) and the mean annual precipitation was 151 mm (± 2.7) (Icelandic Meteorological Office 2016; Unpublished data). Temperature (from 1949-2012) and precipitation (from 1949 – 2008) values were collected from the nearest weather station Fagurhólsmýri (65°53'N, 16°39'W)

1.2 Sampling

In order to uncover the species being dispersed by endozoochory on Skeiðarársandur, I collected dung samples in 2015 from sites on the sand plain where sheep are frequently observed and other sites based on availability. The GPS coordinate location and month of sampling are described in Table 1.A of the Appendix. One sample was collected from each site but the weight of the sample was based on availability, and varied between 0.610 g and 545 g. Eight samples were collected in August and nine in October. A total of 1.06 kg of fresh weight dung was collected in August (mean of 133 g of fresh weight dung per site) and 3.28 kg in October (mean of 364 g of fresh weight dung per site). After collection, dung samples were kept in plastic containers and were stratified for at least eight weeks at 4 °C.

In order to calculate the estimated dry weight for each sample, a small sub-sample was extracted from each total wet dung sample. The subsamples were dried for 72 hours at 70 °C and then weighted. The remaining wet dung samples were homogenized in distilled water. The homogenized wet dung samples were spread out evenly in a thin layer in a plastic tray (22 cm x 17 cm) filled with sterile soil. Depending on the size of the sample, each sample was spread out on one to eight trays. Samples were kept well watered in a green room environment with an temperature of ca. 20 °C and 11 hours of artificial light source, over the course of four months. Trays without dung samples were also included to evaluate the germination of sterile soil and dispersal in the green room.

Once approx. every two weeks, I identified and counted the germinated plant species. Once an emerged specimen was identifiable, it was removed. Otherwise, emerged unidentifiable species were transplanted and given time to mature until identifiable. Emerged specimens that died before identifiable were labeled as “unidentified.” The soil for each sample was micro-tilled in conjunction with the removal of germinated specimens in order to allow more deeply buried seeds to surface and germinate. A plant species was considered to be dispersed via endozoochory if it was found germinating from the dung samples.

1.3 Vegetation Data

To estimate the proportion of species growing in Skeiðarársandur dispersed by endozoochory, a list of vascular plant species growing at Skeiðarársandur was retrieved from a species list generated in 2004/5 and 2012 from 47 permanent study plots on the uppermost part of Skeiðarársandur. Approximately 93 vascular plants were found in these plots (Svavarsdóttir and Þórhallsdóttir, unpublished data).

To identify if dispersed species had any specific characteristics, information on local abundance, classification type of plant species, seed mass, palatability, and mean height was collected. The abundance of the dispersed species was determined by occurrence of the species in the permanent study plots on Skeiðarársandur. The abundance of each species was ranked either common, found in 47 (all) to 32 plots; medium, 31 to 16 plots; or rare, 15 to 0 plots. It is important to note that the 47 study plots are only found in the uppermost part of the sand plain, while some of the sampled sites in this study are outside of the uppermost part of the sand plain. As the sheep can freely graze across the entire sand plain, not limited to the uppermost region, the calculated species abundance might be over- or under- estimated for some species. Likewise, the vegetation survey of the area is limited due to data collected from a narrow geographic location (the 47 study plots in the uppermost sand plain) and not the entirety of the sand plain.

Seed mass values (except *L. nootkatensis*) were obtained from the LEDA Traitbase (Kleyer et al. 2008). Seed mass value for *L. nootkatensis* was based on the SID 7.1 database (Royal Botanic Gardens Kew Seed Information Database (SID), 2016). Sheep preference to dispersed species was obtained from the literature (Thorsteinsson 1980) and each species was marked with either low palatability (1), medium palatability (2), or high palatability (3). If preference information was not available for a specific species, a generalized preference for the genus or the preference for a similar species was used. Information was collected on the primary dispersal methods for the germinated species was based on seed morphology and data on the mean plant height from the local flora (Kristinsson 2010).

1.4 Data Analysis

The data collected from this observational study provides the grounding to conduct a descriptive analysis on the species dispersed by sheep endozoochory and the effectiveness of this dispersal mechanism.

Non-endozoochorically dispersed plant species were identified by subtracting the dispersed plant species from the species list of available vegetation in the Skeiðarársandur area. The seed density of dung dispersion in August and October was calculated using the number of dispersed seeds divided by the total dry weight of dung sample for the month. A linear regression was conducted to detect a possible relationship between the proportion of individual species' specimens to total specimens dispersed variable to seed mass and plant height. To test for significant difference in the seed density between October and August, a t-test was applied to the seed per g^{-1} dry matter for August versus October samples. All statistical analyses and modeling was carried out using MATLAB software (The MathWorks, Inc., Massachusetts, U.S.).

2 Results

In the course of approximately four months, 999 seeds germinated from 24 species in the August and October dung samples. In the August samples, a total of 19 individuals emerged (< 2.0 % total emergence) while in the October samples, 980 individuals emerged (98 % total emergence). In the August samples, 6 species germinated and in October all 24 germinated species were represented. Density of dispersed seeds in the dung samples was 0.17 seeds g^{-1} dry matter in August and 0.58 seeds g^{-1} dry matter in October. We found no significant difference between the seed per g^{-1} dry matter between August versus October samples ($p = 0.57$).

With the germination of 24 species from the dung samples collected in August and October, the sheep dispersed 26 % of the 93 available plant species in the area. Of the 24 species that germinated from the dung samples, 8 were species not found in the 47 permanent plots in Skeiðarársandur. The most common species were *Rumex acetosella* (n = 581), *Agrostis stolonifera* (n = 128), and *Poa pratensis* (n = 73), with the remaining dispersed species having a quantity of less than 25 germinated individuals (Table 1). *Juncus* spp. was most represented in the dispersed species with four individual species identified (Table 1). Of the species dispersed in both August and October, 58 % (36 % of seeds) are classified as graminoids, while 42 % (62 % of seeds) are classified as forbs. No non-herbaceous species (trees and shrubs) were dispersed (Table 1).

None of the dispersed species have special mechanism to promote animal dispersal and most were classified as having unassisted dispersal or combination of unassisted and wind (Table 1). It was found that 54 % of dispersed species (13 % of seeds) were categorized as rare in abundance, while 29 % of species (19 % of seeds) were medium in abundance and 17 % species (68 % of seeds) common abundance.

A majority of dispersed species (83 % of species; 97 % of seeds) has an average height higher than 10 cm. Only 26% of the dispersed species (3 % of seeds) were characterized as having low palatability, while 44% of species (27 % of seeds) had high palatability (Table 1). A range of seed mass values was found for the dispersed species. Seed mass for the dispersed species was in a range from a minimum of 0.0159 mg to a maximum of 2.24 mg (mean seed mass of 0.342 mg ± 0.502). We did not find a correlation between the proportions of individual species' specimens to total specimens dispersed variable to seed mass ($r^2 = 1.2 E -06$, $y = -0.0045x + 0.3417$) and plant height ($r^2 = 0.00056$, $y = -2.9384x + 22.892$).

Table 1. List of species and associated species characteristics that germinated from the sheep dung samples (n=16) collected in August and October 2015 from Skeiðarársandur, in SE Iceland. The Quantity Dispersed reflects the number of identified specimens that emerged from the samples. The Preference reflects the determined palatability on a scale from 1 to 3, with 1 being the most palatable and 3 being the least palatable. The Abundance reflects the number of plots in the area (47 possible) the species was found in. on number of plots (47 in total) that species was found in. Abundance was determined to be Common (47-32 plots), Medium (31-16 plots), or Rare (15-0 plots).

Dispersed Species				Characteristics					
Species	Quantity Dispersed		Classification	Seed mass (*mg*)	Preference	Abundance	Mean Height (*cm*)	Dispersal Method
	Aug	Oct						
Agrostis capillaris	--	8	Graminoid	0.0615	1	Rare	55	Unassisted
Agrostis stolonifera	--	128	Graminoid	0.0270	1	Medium	27.5	Unassisted
Agrostis vinealis	--	20	Graminoid	0.0600	1	Medium	25	Unassisted
Argentina egedii	--	4	Forb	0.8792	2	Rare	5	Unassisted
Campanula rotundifolia	2	1	Forb	0.0670	1	Rare	22.5	Unassisted
Carex maritima	2	48	Graminoid	1.13	2	Common	14	Unassisted
Carex panicea	--	2	Graminoid	2.24	2	Rare	25	Unassisted
Cerastium alpinum	1	3	Forb	0.268	2	Medium	13	Unassisted
Epilobium palustre	--	1	Forb	0.0900	1	Rare	21	Wind
Festuca richardsonii	--	18	Graminoid	0.7890	1	Common	40	Unassisted
Galium normanii	--	2	Forb	0.4290	2	Rare	8.5	Unassisted
Juncus alpinus	--	1	Graminoid	0.0240	3	Rare	22.5	Unassisted
Juncus articulatus	--	9	Graminoid	0.0195	3	Rare	25	Unassisted
Juncus bufonius/ranarius	--	1	Graminoid	0.0254	3	Rare	12.5	Unassisted
Juncus trifidus	--	3	Graminoid	0.1300	3	Medium	16.5	Unassisted
Lupinus nootkatensis	--	5	Forb	0.0159	1	Rare	60	Water
***Luzula* spp.**	--	17	Graminoid	0.335	3	Medium	27.5	Unassisted/Wind
Poa glauca	--	25	Graminoid	0.352	1	Common	25	Unassisted
Poa pratensis	--	73	Graminoid	0.255	1	Rare	45	Unassisted
Rumex acetosella	5	576	Forb	0.364	2	Common	17.5	Unassisted
Sagina saginoides	--	2	Forb	0.0248	NA	Rare	4.5	Unassisted
Thymus Praecox arcticus	1	12	Forb	0.147	2	Medium	3.5	Unassisted
Trisetum spicatum	--	3	Graminoid	0.379	3	Medium	20	Unassisted
Viscaria alpina	8	6	Forb	0.0850	1	Rare	10.5	Unassisted
Unidentified	--	12	NA	NA	NA	NA	NA	NA
Total	19	980						

3 Discussion and Conclusion

Sheep grazing on Skeiðarársandur are key seed dispersal mechanisms through the process of endozoochory, as sheep effectively disperse 25.8% of available vegetation. My results show sheep clearly play a valuable role in local ecosystem functioning by assisting in both existing local plant dispersal and introducing new species to an area of primary succession through long-distance dispersal. Although I did not find any strong patterns suggesting certain plant and seed characteristics impact the dispersal by endozoochory, it is possible with an increased sample size, a relationship between increased dispersal and certain characteristics could be identified. Additionally, it is predicted dispersal through endozoochory in areas of primary succession could benefit from the additional benefits of fertilizer and re-generation niches associated with sheep grazing.

Does the amount of seed dispersed by endozoochory change over the season?

Seed dung density was higher for the October sample (0.58 seed g^{-1} dry matter) than August samples (0.17 seed g^{-1} dry matter). However, we found no significant difference between the seed per g^{-1} dry matter between August versus October samples ($p = 0.57$), suggesting the density of seeds dispersed relative to the weight of dry dung matter was not significantly greater in October as expected. Although, it is likely the lack of significant difference between seasons is due to a small sample size ($n = 16$). As seed maturity in arctic and sub-arctic systems (characterized by cool, short summers and long, cold winters) is usually reached in fall or late fall and seeds do not germinate until the following spring (Bliss 1971), it is assumed the greatest seed density from our sub-arctic environment should have been observed in the October samples. Collection and germination of August dung samples was primarily a method to demonstrate seed dispersal in October (fall months) is greater than in August (or late summer months), when the seeds in the area are not yet mature. Our results suggest sheep serve as an effective seed dispersal mechanism in the period of August to October, however, the role of sheep as a seed dispersal mechanism is still arguably more effective and valuable around October, when more seeds have matured are likely to germinate.

The viable seed density on Skeiðararársandur for the October sample (0.58 seed g^{-1} dry matter) was in the lower range of what other studies on sheep endozoochory have found. Studies looking at endozoochory in grasslands found mean seed densities of 1.2 seeds g^{-1} in the feces of sheep grazing in *Koelerion glaucea* grasslands (Kuiters & Huiskes 2010), 1.1 seeds g^{-1} in dung from sheep grazing in a heathland/grassland mosaic (Mouissie et al. 2005), and 0.2 - 0.6 seeds g^{-1} dry matter of sheep dung from heathland and acidic grassland (Pakeman et al. 2002). When making such comparisons, it is critical to consider the hypothetical vegetation differences in the grassland versus heathland versus primary successional classified sites. Vegetation cover in the compared grassland sites is expected to be much greater than the 10 % or less vegetation cover found in Skeiðararársandur (site of primary succession). When this difference in percentage vegetation cover is taken into account, the seed density found for October samples in Skeiðararársandur is surprisingly high.

What proportion of plant species are being dispersed by sheep endozoochory?

The quantity of dispersed species in relation to total available species (26 %) suggests a considerable portion of the available species can be dispersed by endozoochory and sheep play a critical role in the dispersal of the available vegetation. Similar studies found 43 % of the species (Kuiters & Huiskes 2010) and 37% of the species (Pakeman et al. 2002) in the local species pool were present as viable seeds in sheep dung. In studies on dispersal of Mediterranean grasslands, the percentage of the local species pool having endozoochorously-dispersed seeds varies from 30 % (Malo & Suárez 1995) to 50 % (Traba et al. 2003). Findings from similar studies on the percentage of available vegetation dispersal by endozoochory, indicates endozoochory in Skeiðarársandur dispersed a smaller proportion of the vegetation than expected. However, direct comparison between my results and previous findings on percentage of available vegetation dispersed in highly vegetated or smaller grassland sites may not be an accurate comparison, as we examined a very large and poorly vegetated site with little existing seed pool.

We found that none of dispersed species had been previously classified as using endozoochory as a dispersal mechanism, or any animal assisted dispersal for that matter. The classification, animal assisted dispersal, is likely to be limiting as many species that are not classified as using this means of dispersal, in actuality, utilize animals as a vector for dispersal through the simultaneous ingestion of foliage and small seeds (Janzen 1984). It may be helpful to reconsider the boundaries and classification of animal assisted dispersal, as clearly many unclassified species are dispersed using an animal vector. As this is the first observational study examining the role of endozoochory seed dispersal in Skeiðarársandur, our aim is to merely begin identifying the species that utilize this mechanism of dispersion. The small-scale nature of this study is limited in its observational scope and thus requires additional research to uncover the comprehensive range of species dispersed by endozoochory and characteristics influencing dispersal for the endozoochorically dispersed species.

In areas of primary succession, freely grazing sheep could serve as a long-distance dispersal mechanism and introduce new species to an early emerging plant community with little existing seed pool. As 8 species not previously found in or near the 47 permanent plots in Skeiðarársandur were dispersed by endozoochory, it suggests sheep grazing in this area might serve as critical long-distance dispersing agents. The sheep are possibly able to disperse species not previously found in the representative vegetation of Skeiðarársandur, to colonize new habitat. Although, critical to remember, the species list is limited to the 47 study plots and there are likely more species found on Skeiðarársandur that are not included in the representative vegetation. This long-distance dispersal could be an important contributor to increasing the seed pool and species richness for this area, but equally so, could also result in the unfavorable introduction of foreign and possibly invasive plant species, disrupting the dynamics and species richness of a plant community (Cain et al. 2000). For example, *Lupinus nootkatensis*, a robust and highly invasive species in Icelandic ecosystems, is dispersed by endozoochory, as evidence by our study results. This species had not been previously found in the representative vegetation of

Skeiðarársandur, and thus if introduced by long-distance dispersal through endozoochory, could have a devastating effects on the plant community dynamics and species richness for this area. If a substantial quantity and diversity of seeds are dispersed by herbivores in grazed ecosystems, this could equally so have a significant effect on the species richness of these systems (Pakeman et al 2002). It is critical we further investigate the plant characteristics and factors contributing to dispersal via endozoochory in areas of primary succession, where long-distance dispersal could have a considerable effect on the resulting vegetation succession and diversity.

Do species dispersed by endozoochory have some specific characteristics?

Sheep on Skeiðarársandur seem to be selective in their consumption of available vegetation as more than half of the dispersed species were characterized as rare in abundance (54 %; 13 % of dispersed seeds). The species dispersed by sheep endozoochory are not a random sample of available vegetation, but rather in some capacity "preferentially selected." However, the extent to which the dispersed species are "selected for" is unknown. The dispersed species characteristics examined in this study could provide insight into the factors contributing to selective consumption.

Of the species dispersed, around half were graminoids and half forbs. No non-herbaceous species were dispersed by endozoochory, suggesting mostly or only herbaceous species utilize endozoochory as a dispersal method. From this data, almost an equal proportion of graminoids and forbs species are dispersed by endozoochory, which may indicate no consumption selectivity between graminoid and forb species, but consumption preference of herbaceous species over non-herbaceous species.

Contrary to our hypothesis, the majority of dispersed species (54 %) and seeds (69 %) were low to medium in palatability. The highly palatable species (42 %) and seeds (27 %), which we thought would represent a larger proportion of dispersed species via endozoochory, was less than expected. It is possible we overestimated the effect of palatability and sheep do not have as strong of a palatability consumption preference as previously assumed. Likewise, it is also possible palatability may be site specific, as many of the studies examining sheep palatability, including our study, look at a narrow region (Fischer et al. 1996, Heinken et al. 2002, Malo & Suárez 1995) or one or few species in particular (Bákker & Mouissie 2008).

The results show there is not a link between number of seeds dispersed and seed mass and height of dispersed seeds. Although a majority of dispersed species were over 10 cm in height, indicating that the height of plant species may lead to a morphological advantage to dispersal by endozoochory, we did not find a correlation between proportion of dispersed species and plant height. Previous studies indicate smaller seeds are better able to withstand and escape the molar grinding of ungulate consumption (Pakeman et al. 2002). Smaller seed size also implies shorter retention time during digestion, increased survival rate due to less contact with digestive enzymes, and less contact with microbial attack in ruminal fluids (Pakeman et al 2002). Although a smaller seed mass may lend to a competitive advantage in the dispersal and survival of seeds dispersed by ungulate endozoochory, there was no correlation between the proportion of dispersed species and seed mass. This lack of correlation between proportion of dispersed species and seed mass and plant height is very likely due to the small sample size of this study. However, it might also be that the seeds suitable for endozoochory are not found in the sheep dung.

We did not investigate the typical habitat for each dispersed species, although in the future (and for future nature management decisions) it could prove beneficial to examine the typical habitat and the percentage of vegetation cover for species dispersed by endozoochory and see if any patterns or similarities emerge. For instance we know *Rumex acetosella* typically grows in sparsely vegetated habitats (Kristinsson 2010). *Rumex acetosella* was also the most abundant of dispersed species in this study (n = 581, 58 %). This finding challenges the commonly held belief that freely grazing sheep in Iceland primarily graze in well-vegetated sites, as clearly sheep are dispersing a high quantity of a species found in poorly vegetated habitats.

Conclusion

In the case of Iceland, where there is little diversity of herbivore mammals, but a proportionally high number of freely grazing sheep, the role of the sheep as a seed disperser may significantly impact the plant community dynamics in which it grazes. An assortment of various ungulate species could increase the diversity of a plant community or help restore a plant community, while a single ungulate species, such as the sheep in Iceland, could filter some plant species. Likewise, the long-distance endozoochorous seed dispersal by sheep in Iceland could threaten existing species diversity and richness by the introduction of potentially invasive species, such as *L. nootkatensis*.

Continuing to investigate the impact and extent of sheep endozoochory and examining dispersed seed and plant characteristics, especially in poorly vegetated areas, will result in a better understanding of the filtering mechanism of endozoochory and plant community dynamics. Subsequently, knowledge on sheep grazing tendencies and the filtering mechanism of dispersal via endozoochory will inevitably provide essential insight to make educated decisions regarding the intensity and distribution of sheep grazing in nature management. As land degradation and soil erosion through the loss of vegetation cover and over-grazing is of primary concern in Icelandic nature management, contrary information on currently held assumptions on sheep grazing patterns in Iceland, as a result of examining role of endozoochory on Skeiðarársandur, could lead to improved management decisions and outcomes.

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Appendix

Table 1.A GPS coordinate locations and time of sampling of sites in Skeiðarársandur, SE Iceland

	Month		GPS Coordinates[1]	
Site	*August*	*October*	*East*	*North*
P1	X		587030	385311
P2	X		591398	386835
SKS037	X	X	586288	386064
SKS029	X	X	585746	384095
SKS044	X	X	591854	387777
SKS038	X	X	588244	386069
RÉTT	X	X	590118	386457
BELOW1		X	584215	370902
BELOW2		X	583997	372539
BELOW3		X	583847	374728
BIG HOLE		X	587142	385426

[1] The GPS coordinates of the sites are in the Icelandic grid system (data in ISN93 coordinate system