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## The role of dispersal constraints in the assembly of salt-marsh communities

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*Chapter* 3

**Seed dispersal by small herbivores and tidal water:  
are they important filters in the assembly of  
salt-marsh communities?**

E.R. Chang, E.L. Zozaya, D.P.J. Kuijper & J.P. Bakker

## Summary

Characteristics of internal seed dispersal (endozoochory) by European brown hares were compared to similar dispersal by brent geese. Hares deposited more seeds of mid-successional, perennial, high-marsh species than geese, which deposited more seeds of early-successional, annual, low-marsh species. Seed survival and germination of salt-marsh species were higher after ingestion and passage through the digestive system of hares compared to geese. Both hares and geese had a negative effect on the percentage of seeds that germinated in comparison with uningested seeds. Small herbivores (hares and geese) dispersed two orders of magnitude fewer seeds than those dispersed by tidal water. Thus, they are not likely to be important filters (constraints) in community assembly at this salt-marsh site on a coastal island in the Netherlands.

## Introduction

Community assembly can be conceptualized as a process whereby members of a species pool are eliminated as they pass through a hierarchy of biotic and abiotic filters (Wiens 1983; Keddy 2000). The filters select for certain traits and the species, which form a community, are those with traits that have enabled them to survive passage through the filters. In the case of salt-marsh communities, most research has focussed either on the roles of environmental filters such as salinity (Keddy 2000), or interactions between individuals of the different species such as competition (Wilson & Whittaker 1995; Keddy 2000). Less attention has been paid to the processes that control membership of the species pool.

Dispersal of vegetative diaspores, fruits or seeds is dependent on abiotic (*e.g.* wind, water, rain splatter) and biotic vectors (*e.g.* animals and people). As vectors of seed dispersal, can small herbivores act as important dispersal filters in the assembly of plant communities by determining species pool membership? Studies on the internal dispersal of seeds (endozoochory) by hares, for example, indicate that passage through the digestive system may break dormancy and highly enhance germination in species with hard seed coats (Izhaki & Ne'eman 1997). Rabbits may provide directed dispersal to particularly favourable microhabitats (*c.f.* Howe & Smallwood 1982) in fragmented vegetation communities such as transient wetlands (Zedler & Black 1992). Similarly, mammals and birds disperse seeds of isolated patches of bush-pocket vegetation in dune fields (Castley *et al.* 2001). Rabbits may also facilitate colonization of new habitats such as small disturbances in pastures (Malo *et al.* 1995) and open ground in dune systems (Calviño-Cancela 2002). Endozoochory may be important where high numbers of animals are present, even if the probability of dispersal per individual animal is low, such as is the case with duck species during autumn migration (Charalambidou *et al.* 2003). It may also be important if no other dispersal vector for long distances is available (D'Antonio 1990; Zedler & Black 1992; Milton & Dean 2001).

The effectiveness of endozoochory by small herbivores may change as communities develop and mature. It is predicted that effectiveness will be greater in younger communities where a greater proportion of species are annuals, which depend upon recruitment solely from seed sources, and seed limitation of recruitment is likely to be more prevalent (Turnbull *et al.* 2000). Where other dispersal vectors are present, the importance of endozoochory by small herbivores must be evaluated in relation to the effectiveness of dispersal provided by other vectors. We posed three questions in this study: 1) Do hares and geese differ in their effectiveness as vectors of seed dispersal? 2) Does the effectiveness of hares and geese as seed dispersers change during community development? 3) How effective is endozoochory compared to dispersal by tidal water in an intertidal salt marsh?

## Materials and Methods

### *Site description*

The studies were conducted on the barrier island of Schiermonnikoog, the Netherlands (53° 30' N, 6° 10' E). The island is extending eastward as a consequence of changing sea currents and sediment accretion (Oloff *et al.* 1997). Salt marshes form an age gradient on the southern shore of the island, resulting in a well-developed chronosequence (de Leeuw *et al.* 1993; Oloff *et al.* 1997). Five salt-marsh communities were studied that were characteristic of 10, 15, 30, 40 and 100 year-old marshes. A second gradient, elevation, rises from the intertidal mud flats, across the salt marshes, to the dunes (Oloff *et al.* 1997). Sediments consist of a sandy sub-layer with an upper clay layer (2-16 cm), which increases with community age. Low marshes occur at a sand-layer elevation between 20 - 40 cm above MHT (mean high tide). During the period when this study was conducted, the inundation frequency varied from every few days for young marshes to weekly or bi-weekly for intermediate-aged marshes to infrequent for old marshes. High marshes occur at a sand-layer elevation between 60 - 80 cm above MHT and inundation is infrequent.

About 3000 brent geese (*Branta bernicla bernicla* L.) are residents on Schiermonnikoog between October and late May (Bos & Stahl 2003). Brent geese feed mainly in agricultural pastures but they also graze on the natural salt marshes during the study period in November to December. A range of 30 to 620 brent geese were tallied in this area during monthly counts between October to December from 2001 to 2004 (SOVON Waterfowl counts, Klaas van Dijk & Julia Stahl, unpublished data). Other birds which occur frequently in the area and potentially consume seeds include ducks, such as wigeons (*Anas penelope*), common teals (*Anas crecca*) and mallards (*Anas platyrhynchos*), and passerines, such as snow buntings (*Plectrophenax nivalis*), twites (*Carduelis flavirostris*) and horned larks (*Eromophila alpestris*). About 500 European brown hares (*Lepus europaeus* Pallas) are resident on the natural salt marshes throughout the year (Kuijper 2004).

### *Endozoochorous dispersal by hares and geese*

Seed dispersal in the faeces of hares and geese was estimated by collecting droppings at six sites (three high-elevation and three low-elevation) within each of the five stages of community development. Mean distance between sites was 42 m ( $\pm 25$  standard deviations) and minimum distance was 12 m. At each of the six sites, five marking sticks were placed using *a priori* criteria: high-density patches of *Festuca rubra* for high marshes and high-density patches of *Puccinellia maritima* for low marshes. Plant nomenclature follows van der Meijden (1996). Dropping densities of hares and geese are generally very low and clustered in distribution, and

there is a lot of spatial heterogeneity in structure of the salt marshes. The *a priori* criteria were used to select similar patches, which could be consistently compared along the chronosequence and were feasible candidates to be influenced by endozoochory. For each sampling date, all hare droppings present within a radius of 1.3 m (area = 4 m<sup>2</sup>) from each stick were collected, resulting in a total sampling area of 20 m<sup>2</sup> for each site. Goose droppings were sampled differently from hare droppings due to a lower incidence of occurrence and less even distribution. Goose droppings present within 1.5 m from a direct path between each of the sticks were taken for an average area of 76.24 m<sup>2</sup> sampled for each site. The five sub-samples for each site were pooled. All plots were cleared of droppings on 12 November, 2002. Fresh droppings were counted and collected on 29 November and 12 December, 2002. Data from both sampling dates were pooled and used for all analyses.

Samples were assessed for seed content using a modified seedling emergence technique (ter Heerdt *et al.* 1996). After exposure to a minimum of five weeks of cold stratification (6°C) in order to simulate winter conditions, the samples were transferred to a greenhouse (25°C day temperature, 15°C night temperature, 15-hour light period) and monitored for germination. An additional sample of 100 droppings each for hares and geese was collected and dried in an oven (48 hours, 70°C) in order to express endozoochory samples on a dried mass basis.

#### **Feeding experiments using captive animals**

Five European brown hares born in captivity were used for the feeding experiments. The animals were kept in outdoor pens of 1.5 m x 1 m with a wooden box for shelter and a mesh-wire floor (around 1 cm mesh size) through which droppings could fall onto a net suspended under each cage.

Portions of food were prepared by embedding seeds in a matrix, made of commercial rabbit food pellets softened by immersion in water, and rolling the resulting mixture into a ball. One portion of food was fed to each hare on 16 July, 2002. 50 seeds each of *Suaeda maritima*, *Seriphidium maritimum*, *Glaux maritima* and 30 seeds each of *Elytrigia atherica*, *Plantago maritima* and *Salicornia europaea* were added to each portion. Hares were observed to consume the entire portions. To ensure that all seeds fed to the hares had been excreted, all faeces produced by each hare for one week were collected (Hirakawa & Okada 1995; Hirakawa 2001; Kuijper *et al.* 2004). The droppings collected from the captive hares were processed identically to those collected from the salt marshes. Three control samples of 50 uningested seeds for each plant species were germinated in Petri dishes (similar environmental conditions as ingested samples).

Data obtained from feeding experiments with captive hares were compared to feeding trial data collected from barnacle geese (*Branta leucopsis* L.) on seeds of the same salt-marsh species (Geertsema 2000). Barnacle geese (1780 g) are only

slightly larger than brent geese (1564 g) and share similar food resources (Stahl 2001). About 12 000 barnacle geese reside on Schiermonnikoog between October and early April (Bos & Stahl 2003) but they do not forage on the natural salt marshes between October and December. To our knowledge, no experimental feeding trial data on the effect of brent geese on seed survival and germination exist. Brent geese do not breed in captivity and captive birds are highly susceptible to stress.

#### *Seed dispersal by tidal water*

During approximately the same period when droppings were collected, seed traps were used to measure seed dispersal by tidal water (hydrochory). Seed traps were made of squares of Astroturf® (45 cm x 45 cm) and their efficacy as seed traps is documented in Wolters *et al.* (2004). Seed traps were fastened to the ground using stainless steel pegs.

Ten seed traps were placed at least 10 m apart at each of four stages of community development (40 year-old marsh not sampled) using *a priori* criteria. They were placed in a row parallel to the coastline in the low-elevation sites from where the endozoochorous samples were collected. The traps were set out on 1 November, 2002 and collected seven weeks later on 20 December. After collection, the seed traps were rinsed with water over a 0.212 mm mesh sieve. Very few droppings were observed on the seed traps. The resulting sediment and seed mixtures were then processed identically to the procedure used for dropping samples. In order to facilitate comparisons with endozoochory data, the mean number of seeds collected per 28 days was calculated.

#### *Data analyses*

Germinable seeds recovered from the droppings of hares and geese, and seed traps were analysed using multivariate methods and Monte Carlo permutation tests using the software program, CANOCO for Windows 4.52 (ter Braak & Šmilauer 1998). These analyses parallel analysis of variance (ANOVA). Data from all 14 species found in the droppings were used simultaneously to construct an analysis of variance table, partitioning all the variance explained by sources in the model. Such a table could be conceptually obtained by carrying out an ANOVA on each of the 14 species, totalling the sums of squares (SS) of each ANOVA source across the 14 species, and dividing the resulting sums by the total sum (ter Braak & Šmilauer 1998). The use of Monte Carlo permutations to test the significance of each ANOVA source frees us from an assumption of conventional ANOVA, that of normal distribution, as this is a statistical technique that does not assume a particular distribution. The observed value of a test statistic (F-ratio) for a factor is assessed by comparison to a frequency distribution of expected values under the null hypothesis that is generated by randomly reordering the actual data using some assumed model, not to a theoretical distribution (Manly 1997). The sam-

pling design will determine the assumed model and how data are reordered (permuted). However, the assumption of homogeneity of variance remains.

The sampling design was encoded using dummy variables of 0 and 1. Partial redundancy analysis (RDA) was used instead of partial canonical correspondence analysis (CCA) because partial RDA resulted in better homogeneity of variance in multivariate space, when coupled with a square root transformation, than the partial CCA. Eight separate significance tests using Monte Carlo simulations were run for each analysis, including one for the full model (2 by 5 by 2 full factorial), three main effects (animal type, community state, elevation), three 2-way interactions and one 3-way interaction. For the permutation tests when assessing the main effects, the factor in question was used as the environmental variable and the other two factors were used as covariables. Permutations were restricted by blocks defined by all covariables. In the case of the 2-way interaction tests, all three factors were listed as covariables in the analyses and for the 3-way interaction test, all three factors plus all three 2-way interactions were used as covariables. Permutations for interaction effects were unrestricted. When a factor is used as a covariable in an analysis, only the variability explained by the environmental variables after subtracting overlapping variance explained by the covariables is considered. For figures illustrating significant factors, parsimonious models are shown. A practical guide to setting up similar analyses in CANOCO is given in this paper. For more technical and theoretical discussions, consult ter Braak & Šmilauer (1998) and Lepš & Šmilauer (2003). For further discussions on Monte Carlo tests, consult Manly (1997) and Edgington (1986).

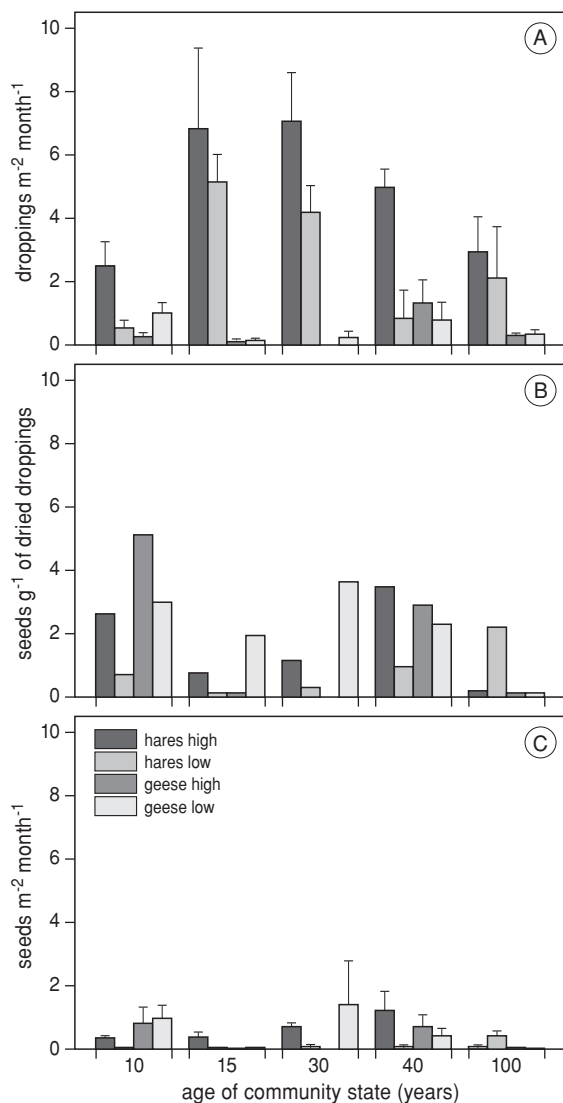
When the distribution of a data set is non-normal, one can either transform the data to meet the model assumptions or one can conversely mould the model to meet the data characteristics, which is what occurs in generalized linear models (Crosbie & Hinch 1985). For the feeding trials, a general linear model ANOVA was used with animal type and seed species as fixed factors using SPSS 12.0.1 for Windows (2003). A square-root transformation was used to meet model assumptions. For endozoochorous and hydrochorous data, generalized linear models using Poisson distribution were used to analyse univariate data pooled for all species using S-Plus 6 Professional (2001).

## Results

### *Endozoochorous dispersal by hares and geese*

Hares deposited a significantly higher number of droppings per unit area than geese (Fig. 3.1A) (generalized linear model,  $F_1 = 67.4$ ,  $p < 0.01$ ). More droppings were found in high marshes than in low marshes per unit area (generalized linear model,  $F_1 = 6.1$ ,  $p = 0.02$ ).





**Figure 3.1** Distribution of hare and goose droppings, and seeds found in these droppings along a chronosequence of plant communities at high and low elevations; error bars represent standard errors: A) mean number of droppings per square metre deposited in a month (28 days); animal type and the elevation were significant factors, B) mean number of seeds (all species pooled) found per gram of dried hare and goose droppings; no factors were found to be significant, and C) mean number of seeds (all species pooled) found per square metre in a month; only the interaction factor between animal type and elevation was significant.

When the data for all plant species were pooled, no significant trends were seen in the number of seeds found per gram of dried hare and goose droppings (Fig. 3.1B). However, when multivariate data were considered, there was a highly significant difference between the composition of germinable seeds found per gram of dried hare and goose droppings ( $SS = 0.15$ ,  $F_{1,46} = 10.28$ ,  $p < 0.01$ ), a highly significant effect of where the seeds occurred along the community state sequence ( $SS = 0.15$ ,  $F_{4,49} = 2.46$ ,  $p < 0.01$ ) and also a significant interaction effect between community state and animal type ( $SS = 0.10$ ,  $F_{4,44} = 1.70$ ,  $p = 0.04$ ). Except for the 10 year-old community state, the most abundant species found in hare droppings was *Seriphidium maritimum* (Table 3.1). Seeds found in goose droppings were dominated by annuals such as *Salicornia europaea* and *Suaeda maritima* except for samples taken from the oldest community state.

When data were pooled for all species, the average number of seeds found per square metre showed only a significant interaction effect between animal type and elevation (generalized linear model,  $F_1 = 4.68$ ,  $p = 0.04$ ) (Fig. 3.1C). Hares deposited more seeds in high marshes than in low marshes, in contrast to geese which deposited more seeds in low marshes. When multivariate data were considered, there was a highly significant difference in species composition between seeds deposited by hares and by geese ( $SS = 0.12$ ,  $F_{1,54} = 8.59$ ,  $p < 0.01$ ). Hares deposited more seeds of mid-successional, perennial, dicotyledonous species such as *Seriphidium maritimum* and *Plantago maritima*. In contrast, geese dispersed more seeds of early-successional, annual, dicotyledonous species such as *Salicornia europaea* and *Suaeda maritima* (Table 3.1) (Fig. 3.2B). There was also a highly significant effect of community state on the species composition of the deposited seeds ( $SS = 0.13$ ,  $F_{4,57} = 2.28$ ,  $p < 0.01$ ). The first RDA axis (Eigen-value = 0.171), which is much stronger than the second axis (Eigenvalue = 0.046), separated the samples found in the youngest community state from the other community states (Fig. 3.2B). Droppings deposited on the youngest community state were mostly composed of the early-successional, annual species listed above. All older community states (age 15 to 100) could not be readily distinguished from each other based upon seeds dispersed by hares and geese.

#### ***Feeding experiments using captive animals***

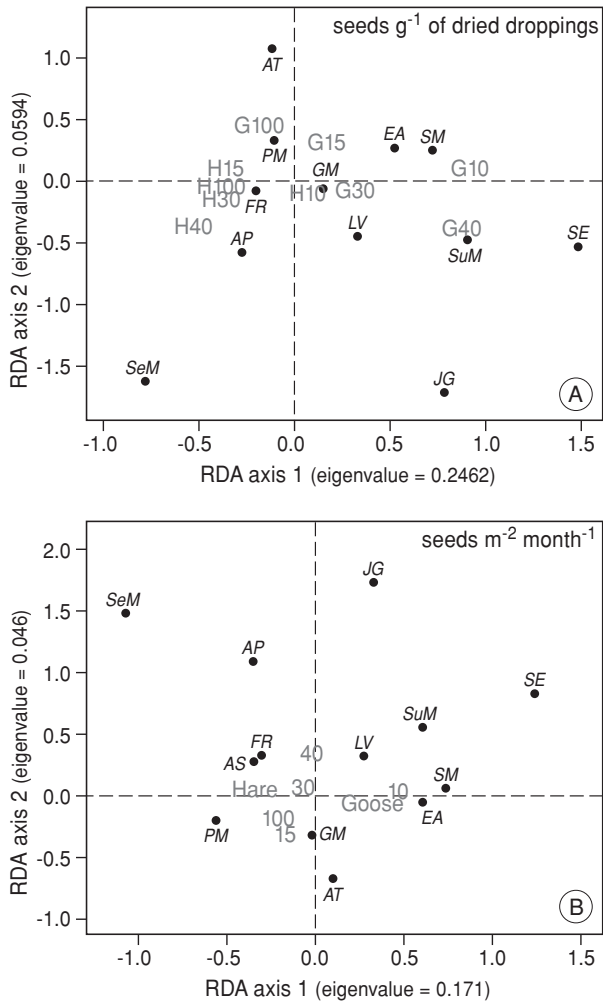
Relative germination percentage (absolute mean germination percentage / mean germination percentage of control seeds) was used to compare the feeding trial data collected from hares and geese because different control samples were used in the two experiments. A significantly greater percentage of seeds survived passage through the digestive system of European brown hares compared with that of barnacle geese (Fig. 3.3) (ANOVA,  $F_{4,33} = 35.98$ ,  $p < 0.01$ ). There were no significant differences in survival between seeds of the five species.

**Table 3.1** Density of germinable seeds found in brent goose and European brown hare droppings (seeds  $m^{-2} month^{-1} \pm$  standard error) in five stages of community development. Both high-elevation and low-elevation marshes were sampled at each of the five stages.  $n = 3$

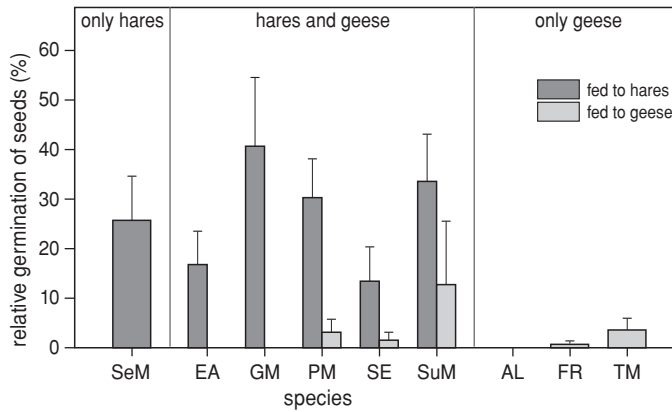
Species	10 year-old community				15 year-old community				30 year-old community					
	Hares		Geese		Hares		Geese		Hares		Geese			
	High	Low	High	Low	High	Low	High	Low	High	Low	High	Low		
<i>Agrostis stolonifera</i>	0	0	0.13 $\pm 0.013$	0	0	0	0	0	0	0	0.17 $\pm 0.12$	0	0	0
<i>Aster tripolium</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Atriplex prostrata</i>	0.033 $\pm 0.033$	0	0	0	0	0	0	0	0	0	0.12 $\pm 0.093$	0	0	0
<i>Elytrigia atherica</i>	0	0	0.0043 $\pm 0.0043$	0	0	0	0	0	0	0	0	0	0	0
<i>Festuca rubra</i>	0	0	0	0	0	0	0	0	0	0	0.017 $\pm 0.017$	0	0	0
<i>Glaux maritima</i>	0.15 $\pm 0.10$	0	0.017 $\pm 0.017$	0	0.033 $\pm 0.017$	0	0.0051 $\pm 0.0051$	0	0	0	0	0	0	0
<i>Juncus gerardii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0043 $\pm 0.0043$
<i>Limonium vulgare</i>	0	0	0	0.0097 $\pm 0.0048$	0	0.017 $\pm 0.017$	0	0	0	0	0	0	0	0.013 $\pm 0.0075$
<i>Plantago maritima</i>	0	0	0.017 $\pm 0.011$	0	0.083 $\pm 0.017$	0	0	0	0	0.12 $\pm 0.093$	0.017 $\pm 0.017$	0	0	0
<i>Salicornia europaea</i>	0.05 $\pm 0$	0.03 $\pm 0.03$	0.16 $\pm 0.090$	0.87 $\pm 0.37$	0	0	0	0.027 $\pm 0.027$	0	0	0.017 $\pm 0.017$	0	0	1.0 $\pm 1.0$
<i>Seriphidium maritimum</i>	0.13 $\pm 0.13$	0	0	0	0.23 $\pm 0.18$	0.017 $\pm 0.017$	0	0	0	0.22 $\pm 0.060$	0.05 $\pm 0.029$	0	0	0.10 $\pm 0.10$
<i>Spergularia media</i>	0.017 $\pm 0.017$	0	0.43 $\pm 0.34$	0.073 $\pm 0.073$	0.017 $\pm 0.017$	0	0	0	0	0	0	0	0	0
<i>Suaeda maritima</i>	0	0	0.18 $\pm 0.13$	0.0097 $\pm 0.0097$	0	0	0	0	0	0.033 $\pm 0.033$	0	0	0	0.25 $\pm 0.25$

Table 3.1 Continued

Species	40 year-old community				100 year-old community				
	Hares		Geese		Hares		Geese		
	High	Low	High	Low	High	Low	High	Low	
<i>Agrostis stolonifera</i>	0	0	0	0	0.017 ±0.017	0	0	0	0
<i>Aster tripolium</i>	0	0	0	0	0	0	0	0.010 ±0.010	0
<i>Atriplex prostrata</i>	0.017 ±0.017	0	0.012 ±0.0070	0.0043 ±0.0043	0.017 ±0.017	0	0	0	0
<i>Elytrogia atherica</i>	0	0	0	0	0	0	0	0	0
<i>Festuca rubra</i>	0	0	0	0	0	0	0	0	0
<i>Glaux maritima</i>	0	0	0	0	0	0.017 ±0.017	0	0	0
<i>Juncus gerardii</i>	0.017 ±0.017	0	0.10 ±0.098	0.035 ±0.019	0	0	0	0	0
<i>Limonium vulgare</i>	0	0	0.0084 ±0.0084	0.013 ±0.0075	0	0.017 ±0.017	0	0	0
<i>Plantago maritima</i>	0	0	0	0	0	0	0	0	0
<i>Salicornia europaea</i>	0	0	0.48 ±0.26	0.31 ±0.23	0	0	0	0.01 ±0.01	0
<i>Seriphidium maritimum</i>	1.1 ±0.65	0.067 ±0.017	0.059 ±0.041	0	0.017 ±0.017	0.30 ±0.18	0	0	0
<i>Spergularia media</i>	0.033 ±0.033	0	0	0	0	0.017 ±0.017	0	0	0
<i>Suaeda maritima</i>	0.017 ±0.017	0	0.067 ±0.034	0.022 ±0.022	0	0.05 ±0.05	0	0.021 ±0.021	0



**Figure 3.2** Biplots of species and environmental centroids illustrating significant factors in two multi-species analyses of variance (ANOVA). Partial redundancy analysis (RDA) was used based upon seed data constrained by the design (3-way ANOVA). The parsimonious models are shown. Seed data were transformed using  $y = \sqrt{x}$ . Species abbreviations are: AS = *Agrostis stolonifera*, AP = *Atriplex prostrata*, AT = *Aster tripolium*, EA = *Elytrigia atherica*, FR = *Festuca rubra*, GM = *Glaux maritima*, JG = *Juncus gerardii*, LM = *Limonium vulgare*, PM = *Plantago maritima*, SE = *Salicornia europaea*, SeM = *Seriphidium maritimum*, SM = *Spergularia media*, SuM = *Suaeda maritima*. A) Ordination diagram of mean number of seeds found per gram of dried droppings. Animal type, community state and their interactions were found to be significant. Only the interaction factors are shown: H = hare, G = goose; numbers refer to age of community. B) Ordination diagram of mean number of seeds found per square metre. Only the main effects of animal type and community state were found to be significant. Numbers refer to the age of the community.



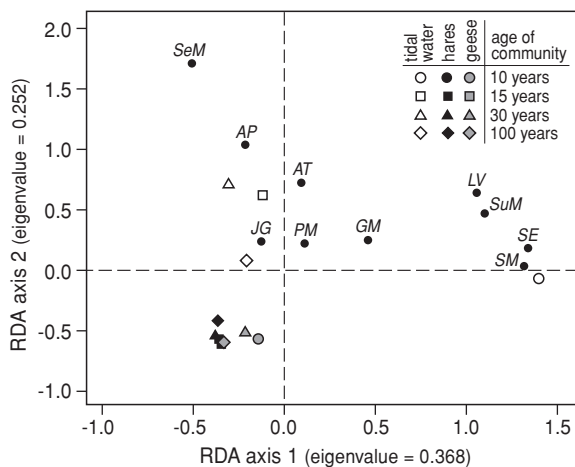
**Figure 3.3** The germination of seeds after passage through the digestive systems of captive European brown hares and barnacle geese. Seeds of some species were fed only to hares, others to the geese and five species were fed to both. The mean germination percentages were corrected by dividing by the percentage of uningested seeds germinating for each species. Error bars represent standard errors. In addition to the species abbreviations used in Figure 3.2: AL = *Atriplex littoralis*, TM = *Triglochin maritima*.

**Table 3.2** Density of seeds dispersed by tidal water (seeds m<sup>-2</sup> month<sup>-1</sup> ± standard error) in four stages of community development. Only low-elevation marshes were sampled. n = 10

Species	10 year-old community	15 year-old community	30 year-old community	100 year-old community
<i>Aster tripolium</i>	0.55±0.37	6.9±4.5	1.1±0.84	0
<i>Glaux maritima</i>	0.28±0.28	0.28±0.28	0.28±0.28	
<i>Juncus gerardii</i>	0	0.28±0.28	0	0.28±0.28
<i>Limonium vulgare</i>	74±19	28±15	6.9±6.0	24±17
<i>Plantago maritima</i>	0.28±0.28	1.4±1.4	0	0.28±0.28
<i>Salicornia europaea</i>	310±99	3.3±1.5	14±13	10±9.9
<i>Seriphidium maritimum</i>	0	280±150	590±100	130±85
<i>Spergularia media</i>	14±5.5	0.55±0.37	0	0.55±0.55
<i>Suaeda maritima</i>	130±71	2.2±1.2	65±38	8.0±6.4

**Comparison of seeds dispersed by endozoochory and tidal water**

The type of dispersal vector had a highly significant effect upon numbers and composition of dispersed seeds (SS = 0.24, F<sub>2</sub> = 14.03, p < 0.01). Many more seeds were dispersed by hydrochory than were dispersed by endozoochory (Tables 3.1 & 3.2). The community state where seeds were dispersed also had a significant effect, both when considering pooled data for all species (generalized linear



**Figure 3.4** Biplot of species and environmental centroids illustrating significant factors in a multi-species analysis of variance (ANOVA) comparing seed dispersal by hydrochory and those dispersed internally by hares and by geese. Partial redundancy analysis (RDA) was used based upon seed data constrained by the design (2-way ANOVA). The parsimonious model is shown. Seed data were transformed using  $y = \log_{10}(x + 0.01)$ . Species abbreviations are the same as in Figure 3.2. The vector type, the community state where the seeds were found and their interactions were found to be significant. Only the interaction factors are shown. See inset key for explanation of symbols.

model,  $F_2 = 5.04$ ,  $p = 0.03$ ) and when considering the multivariate data ( $SS = 0.261$ ,  $F_3 = 10.12$ ,  $p < 0.01$ ). When using multivariate data for all species, there was also a highly significant interaction effect between vector type and community state ( $SS = 0.14$ ,  $F_6 = 3.32$ ,  $p < 0.01$ ); *i.e.* there was a significant effect of community state for hydrochorous samples but not for endozoochorous samples. The first RDA axis separated samples dispersed by tidal water at the 10 year-old community state from the rest of the samples (Fig. 3.4). These samples contain many seeds of annual species such as *Salicornia europaea*, *Spergularia media* and *Suaeda maritima*. The second RDA axis distinguished three groups: samples dispersed by hydrochory at intermediate community states (15 and 30 year-old) containing many seeds of *Seriphidium maritimum*, samples dispersed by hydrochory at the youngest and oldest community states (10 and 100 year-old) and samples dispersed by endozoochory. For the samples dispersed by hydrochory, the community state has an important effect upon both seed number and species composition unlike samples dispersed by endozoochory. Note that all species in the biplot are associated with centroids of hydrochorous sample groups rather than with endozoochorous sample groups, signifying that small amounts of seeds of all species are dispersed by endozoochory in comparison with hydrochory.

## Discussion

### *Differences in effectiveness of seed dispersal by hares and geese*

When considering all the salt-marsh communities together, hares and geese dispersed similar quantities of seeds. However, they dispersed seeds of different species and to different types of habitats. The most common species found in hare droppings was *Seriphidium maritimum*, a mid-successional, perennial species. In contrast, goose droppings contained mostly early-successional, annual species such as *Salicornia europaea* and *Suaeda maritima*. Hares deposited seeds more often in high marshes, whereas geese deposited seeds more often in low marshes reflecting their grazing preferences. For example, brent geese feed on *Salicornia europaea* in autumn (Summers *et al.* 1993; Bruinzeel *et al.* 1997). In studies conducted at Schiermonnikoog, brent geese graze preferentially in low-elevation *Puccinellia maritima* marshes (van der Wal *et al.* 1998) of intermediate age (Olf *et al.* 1997) whereas hares graze more often on higher *Festuca rubra* marshes (van der Wal *et al.* 1998). Whereas patterns in endozoochory reflected the grazing preferences of the animals, they did not directly correspond to the plant distribution along the community state sequence suggesting that these small herbivores are selective grazers. Regressions between seed density of droppings and both frequency in the vegetation and seed production yielded non-significant results.

An important component used to determine the quality of seed dispersal by animals is the treatment of seeds in the mouth and gut. The experimental feeding trials indicate that seeds suffer from less damage in the digestive system of European brown hares than that of barnacle geese. The relative percentage of seeds that germinated after passage through hares ranged from 13.6 % to 42.3 %. When compared to studies using rabbits, these numbers are much higher than the percentages reported for species found in North American sagebrush-grasslands and salt-deserts (0 - 5.2 %) (Lehrer & Tisdale 1956) but comparable to species found in temperate West European grasslands (1.2 - 30.5 %) (Cosyns *et al.* 2005). In comparison with hares, a lower percentage of seeds germinated after ingestion by geese (0% to 12.8%). In a recent review on feeding trials of waterbirds, the effects of digestion on the seeds of aquatic and wetland species were found to be highly variable (Charalambidou & Santamaria 2002). Although hares physically damage their food by chewing and reingesting their faeces for a second time (Hirakawa 2001), seeds passing through the digestive systems of geese receive the most physical damage in the gizzard (Charalambidou & Santamaria 2002). Apparently, seeds are more damaged passing once through the gizzards of geese than being chewed and digested multiple times by hares. This is a surprising result as geese show less efficient digestion of food (10 to 40 % for cellulose, 25 to 40 % for protein) (Bruinzeel *et al.* 1997) than hares (40% and 60% respectively for dry matter and nitrogen) (Kuijper *et al.* 2004).



### ***Changes in effectiveness of seed dispersal as communities develop***

At early stages of community development, geese were more effective as dispersal vectors relative to hares. The composition of seeds found in the droppings of geese dominated the droppings found at the 10 year-old community state as hare droppings were uncommon (Fig. 3.2B). The predominantly annual species dispersed by geese are obliged to recruit from seeds in order to persist in these community states. Seeds of perennial species associated with goose droppings, such as *Limonium vulgare* and *Elytrigia atherica*, were present in very low numbers. Hares were relatively more important than geese in intermediate and older community states as dispersal agents. The predominantly perennial species dispersed by hares, however, are less dependent on seed input for persistence in these communities because of clonal growth. The only exception was *Atriplex prostrata*, an annual species found in older, more nutrient-rich community states but it occurred in very low numbers in droppings.

Species may be present in the actual or community species pool (Zobel *et al.* 1998) as an adult plant, in a diaspore bank or in the diaspore rain. During the assembly process of young communities, community species pool membership may be more constrained by seed input than in older communities. Thus, geese were judged to be more effective as dispersal vectors than hares.

As young, low communities were more frequently inundated than other communities, it is possible that there was an under-estimation of endozoochory to these sites. Faeces may dissolve or be re-dispersed more quickly than the time between sampling dates (two weeks). In this case, however, the conclusion that geese were more effective dispersal vectors than hares would only be reinforced.

### ***Seed dispersal by small herbivores versus dispersal by tidal water***

When considering the quantity of germinable seeds dispersed, small herbivores dispersed fewer seeds than numbers dispersed by tidal water on the low marshes by two orders of magnitude (Tables 3.1 & 3.2). Also, there is no evidence that small herbivores dispersed any species that were not dispersed by tidal water (Tables 3.1 & 3.2) (Fig. 3.4). All the species in the species-environmental centroids biplot are associated with the seed trap sample groups rather than with the endozoochorous sample groups.

Is there any indication that small herbivores provide better quality of seed dispersal with respect to seedling establishment than tidal water? Izhaki & Ne'eman (1997) concluded that the small amount of dry matter in faeces produced by hares in a sandy, coastal plain environment did not provide sufficient nutrients to enhance seedling establishment. No seedlings were observed germinating in intact droppings during the course of this study. However, faeces produced during the wet months of autumn are likely to disintegrate quickly, although the rate has not been studied. Any nutrient pulse is likely to be very transient compared to that

provided by the dung of large herbivores, although seeds dispersed by small herbivores may also escape the negative effects of manure, such as toxicity for seedlings and low affinity for water (Malo & Suárez 1995) and severe seedling competition due to high numbers of seeds being defecated together (Traveset 1998).

Water, especially during storm surges, is not a very selective agent of seed dispersal and results often in deposition of seeds in the driftline along the dunes, that provide poor-quality microsites for salt-marsh species. Many seeds embedded in the droppings of hares and geese will undergo secondary dispersal by water. High numbers of droppings have been observed in driftlines at this site. In summary, it is not likely that small herbivores provide enough higher quality seed dispersal with respect to suitable microsite to make an important impact on seed dynamics in these marshes.

Small herbivores could still be important filters in salt-marsh assemblages if they act as agents of long-distance dispersal; that is distances greater than 100 m (Ozinga *et al.* 2004). These low-probability events have the potential for a high impact on community assembly as in the case of colonization of new habitats. A recent review on the possibilities of long-distance endozoochorous dispersal by migratory waterbirds in northern Europe (Clausen *et al.* 2002) identified some potential hurdles which led the authors to conclude that such events were likely to be rare, whereas two other reviews from the same year (Figuerola & Green 2002; Green *et al.* 2002) were more positive. However, some of the hurdles identified in Clausen *et al.* (2002) may not be problematic in our system because: 1) reproductive efforts of salt-marsh plants are well-matched with long-distance movements of brent geese (mid-to-late September); 2) gut contents of birds being discarded within 300 km is well above our defined lower limit for long-distance movement (*i.e.* 100 m); and 3) migrating brent geese move between similar habitats along the Dutch Wadden Sea.

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