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Endozoochorous seed dispersal by Korean water deer (*Hydropotes inermis argyropus*) in Taehwa Research Forest, South Korea

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ABSTRACT

Endozoochorous seed dispersal by ungulates can facilitate the dispersal of seeds over long distances. Endozoochorous seed dispersal can also result in the ecological filtering of plant species by dispersing plant seeds with distinctive traits. The Korean water deer (Hydropotes inermis argyropus) is a potential long-distance seed dispersal vector in lowland areas of South Korea. In this study, to test the endozoochorous seed dispersal role of Korean water deer in forested areas, we collected 202 fresh fecal pellet group samples in Taehwa Research Forest, Gwangju City, Gyeonggi Province, South Korea. Additionally, we conducted a vegetation survey to compare the traits of dispersed seeds from feces with the seed traits of flora in the study site. To test whether the composition of species traits dispersed by endozoochory is consistent with that of lowland areas, which consist of forested hills, arable land, and wetlands, we compared the results with a former study conducted in the lowlands. From the seedling emergence method applied to feces, we found a total of 22 species and 115 seedlings. Among 202 fecal pellet groups, 19.8% had at least one germinable seed. Species of forbs, with small-sized seeds ($\leq 2 \text{ mm in length}$), from open habitat, and seeds without special morphology for dispersal are most frequently dispersed through Korean water deer endozoochory. These traits were consistent with the former endozoochory study conducted in a lowland area, irrespective of the different available flora. Therefore, we suggest that deer can potentially disperse seeds with the aforementioned traits to forest plant communities, acting as a consistent ecological filter through endozoochory.

1. Introduction

Through seed dispersal, plant species can move and colonize new suitable habitats (Cain et al., 2000). Long-distance dispersal is particularly important for maintaining plant species populations and for facilitating plant adaptation to rapid environmental changes such as habitat fragmentation and climate change (Cain et al., 2000; McConkey et al., 2012). Endozoochory, the dispersal of seeds through ingestion and defecation by animals, allows seeds to disperse over long distances (Vellend et al., 2003; Nathan et al., 2008; Soons et al., 2008). Of these animals, ungulates have large home ranges and are distributed across a wide variety of ecosystems; therefore, ungulates are regarded as important vectors for long-distance seed dispersal (Baltzinger et al., 2019).

During the seed dispersal process, seeds are consumed, transferred by animals and deposited in new sites (Cain et al., 2000; Baltzinger et al., 2019). At each stage, the traits of both plants and animals affect the success of seed dispersal (Schupp, 1993;

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Baltzinger et al., 2019). The number of seeds consumed by animals and the number of times they visit the plants can determine the quantity of seeds dispersed. When animals visit an area to feed, their feeding selectivity and diet affect the degree of seed predation (e. g., Karimi et al., 2018; Picard et al., 2016). Subsequently, when seeds are being transferred by animals, the survival of seeds during gut passage affects seed dispersal success. The way how the seeds survive thermally and chemically harsh environments experienced when passing through the gut of animals, and the time this passage takes can be used to qualitatively determine the survival rates of seeds (e. g., Picard et al., 2015; Milotić and Hoffmann, 2016).

Ungulates have a varied plant diet composition depending on the grazing site (roe deer, Cornelis et al., 1999; red deer, Gebert and Verheyden-Tixier, 2001; Korean water deer, Kim et al., 2011). Consequently, the species dispersed via endozoochory by a given ungulate species in different habitats is linked to different compositions of plant communities (Yamashiro and Yamashiro, 2006). However, the traits of seeds dispersed by ungulates through endozoochory usually have a similar pattern, irrespective of the plant species pool (Picard et al., 2016). Small, round, light seeds are more likely to be rapidly consumed and defecated (Cosyns and Hoffmann, 2005; Pakeman et al., 2002). Additionally, hard seeds are likely to endure the harsh environment when passing through the gut (Gardener et al., 1993). Seed size and seed dormancy forms also affect the process of endozoochory (Jaganathan et al., 2016; Soltani et al., 2018). Dispersing plant species with distinctive traits suggest that the seed dispersal mechanism of ungulates functions as an ecological filter for plant communities (Albert et al., 2015). Meanwhile, the seed production in a specific region is subsequently reflected in the number of plant species and seedlings found in the feces (Malo and Suárez, 1995). Thus, the seasonal patterns of seed production in specific regions are often manifested through seasonal patterns in endozoochory (e.g., Kuiters and Huiskes, 2010; Lee and Lee, 2020).

The Korean water deer (*Hydropotes inermis argyropus*) is the most abundant wild ungulate species on the Korean peninsula. The deer occupies a wide range across the peninsula from the mountains to the lowlands (Kim et al., 2016). The deer species has been identified as a potential endozoochorous seed dispersal vector in the lowlands of South Korea, consisting of a mosaic of low hill forests, arable land, and wetlands (Lee and Lee, 2020). The species mainly disperse forbs, species from open areas, and species ≤ 2 mm seed length (Lee and Lee, 2020). The diet composition of Korean water deer differs between habitats; they consume more woody species in forested areas and more forbs and graminoids in the lowlands (Kim et al., 2011, 2021). Therefore, we hypothesize that the dietary differences derived from vegetation differences between sites will have an impact on the endozoochory potential of Korean water deer and plant species found in the feces would be different in forested and lowlands areas. However, as the gut passage restrains species that can be potentially dispersed through endozoochory, the trait composition of dispersed species should show a similar pattern, regardless of vegetation composition. Therefore, in this study, to test the endozoochorous seed dispersal pattern of Korean water deer, we sampled the fecal pellet groups of water deer in the Taehwa Research Forest (TRF), Gwangju City, Gyeonggi Province, South Korea and conducted a vegetation survey. We identified the species and number of germinable seeds, tested for a seasonal dispersal pattern in number of species and seedlings, and compared the composition of species traits between both regional flora and species found in the feces. In addition, these results were taxonomically and functionally compared with those of our previous study on Korean water deer endozoochory in the lowlands (CCZ) of South Korea (Lee and Lee, 2020).



Fig. 1. Sampling site of fecal pellet groups of Korean water deer. The left image was obtained from Google Earth (Google Inc., 2015).

2. Materials and methods

2.1. Study site and feces sampling

We sampled the feces of Korean water deer in the Taehwa Research Forest (TRF), which is associated with Seoul National University, located in Gwangju City, Gyeonggi Province, South Korea (37°18′34″ N, 127°18′07″ E) (Fig. 1). The area is approximately 795 ha, originally established as a research forest in 1979, with an altitude of 150–641 m above sea level (https://uf.snu.ac.kr/#/introduction). The TRF consisted of natural forest and plantations. The plantations comprised of *Larix kaempferi* and *Pinus koraiensis*, while the natural forests include oak species (e.g., *Quercus mongolica, Q. acutissima, Q. variabilis*), *Fraxinus rhynchophylla*, and *Prunus sargentii* (https://uf.snu.ac.kr/#/status). Some open-area species were present along the edges of the forest management roads. Moreover, since access to the TRF is limited for research purposes only, the site was adequate for sampling fresh fecal pellet groups of the water deer. We sampled 202 fecal pellet groups from April 2017 to March 2018 by sampling at least 10 fresh fecal samples each month. After collection, the samples were air-dried at room temperature, and the dry material was weighed and stored in a cold room for cold treatment for at least three months.

2.2. Germination test

For seed germination, we applied the overall seedling emergence method. We followed the same protocol used in our previous study on Korean water deer endozoochory (Lee and Lee, 2020). The sampled fecal pellet groups were tested for germination by spreading the feces of the Korean water deer in individual pots with soil. Ten control pots were used to monitor outer soil contamination. Seed germination was monitored for three months and pots were regularly watered. Subsequently, to facilitate the germination of some plant species (Kuiters and Huiskes, 2010), the pots were left un-watered for the first three weeks, and then kept moist by regular watering for an additional eight weeks until the end of the trial. The germinated seedlings were identified to species when possible, during the experimental period. Unidentified species were grown in separate pots for longer periods to facilitate species identification. No seedlings germinated from the control pots.

2.3. Vegetation survey

To compare the composition and functional traits of species from vegetation in the TRF and those found in the feces of Korean water deer, we conducted a vegetation survey in July and August, 2019. We set out thirty-eight $10 \times 10 \text{ m}^2$ vegetation plots to cover the overall vegetation structure available in the study area and conducted a vegetation survey. Each of the vegetation plots were placed at a minimum distance of 60 m, to a maximum distance of 3.6 km. We tried to investigate the overall flora that was available at the study site. The species abundance from canopy layer to herbaceous layer is listed following the Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1964). All species found from the vegetation survey were combined in order to investigate the available flora in the study site (Supplementary data; Supplementary Table 3).

2.4. Data analysis

Germinated seedlings were identified at the species level when possible; otherwise, the seedlings were assigned to a genus or family. The functional traits of the identified species were also investigated in further analyses. These functional traits included plant growth form, habitat type, seed length and diaspore morphology. Each functional trait was determined with reference to Choung et al. (2012), the Korean Biodiversity Information System (http://www.nature.go.kr) for habitat type (aquatic, cultivated species, forest, meadow and shrublands, wet meadow), and the Korea National Arboretum (2017), Asano (1995), Fire Effects Information System, National Institute of Ecology (2016), and Korea Research Institute of Bioscience and Biotechnology (2009) for seed length. Seed length was divided into three categories: small (for seeds <1 mm), medium (1–2 mm), and large (>2 mm). Finally, the diaspore morphology types were categorized according to morphology; including presence of elaiosome, ballistic, no special morphology, fleshy/edible fruit, wind, and hooked. These types were determined with reference to the Korea National Arboretum (2017), Asano (1995), the Korea Research Institute of Bioscience and Biotechnology (2009) and Kattge et al. (2011).

The differences in the proportion of each trait category between species from the vegetation survey and the fecal pellet group (in terms of species presence, rather than species abundance) were tested using Fisher's exact test. Unidentified species or species without trait information were excluded from further analyses. In addition, to compare the species' traits from regional flora and species from germination tests in the lowland areas, we used the data from Lee (2020) and tested the differences using Fisher's exact test. The study site used by Lee and Lee (2020) was the lowland areas of CCZ, which has low forested hills, arable land, and wetlands with an altitude of 0–116 m above sea level (Supplementary Table 1).

The seasonal differences in both the number of seeds and species per fecal pellet group were tested using a Kruskal–Wallis test [Spring: April to June (64 fecal pellet groups), Summer: July to September (45 fecal pellet groups), Fall: October to December (45 fecal pellet groups), Winter: January to March (48 fecal pellet groups)]. All graphs were generated using the package "ggplot2" (Wickham, 2016). All analyses were conducted using R version 4.2.1. (R Core Team, 2020).

3. Results

Of a total 202 fecal pellet groups, 40 (19.8%) had at least one germinable seed. From these groups, we have found a total of 115 seedlings that accounted for 15 families, 21 genera and 22 species with a maximum seedling number of 18 seedlings per fecal pellet group. Overall, 0.6 seeds germinated per pellet group and 10.3 seedlings germinated per 100 g of feces. The most abundant species found in the fecal pellet group was *Chenopodium album*, accounting for 26 seedlings (22.6% of total no. of seedlings). The second-most prevalent species were *Portulaca oleracea* and *Solanum americanum*, accounting for 13 seedlings for each species (11.3% of total no. of seedlings) (Table 1).

Among the four seasons, no differences in either the number of seedlings (P = 0.9590; $\chi^2 = 0.30532$; df = 3; Kruskal–Wallis test) or species per fecal pellet group (P = 0.9586; $\chi^2 = 0.30765$; df = 3; Kruskal–Wallis test) were found.

When we compared the traits of plant species between the species from the fecal pellet group and the vegetation data, their composition differed in all species traits tested (Fig. 2). The proportions of growth forms found in feces and flora differed significantly

Table 1

List of total seedling numbers of plant species germinated from the feces of Korean water deer in Taehwa Research Forest. Asterisks indicate species that also germinated from the feces of Korean water deer in lowland areas (Lee and Lee, 2020). Seed length categories are shown in parentheses (S, <1 mm; M, 1–2 mm; L, >2 mm).

Species			Total number of seedlings	Number of fecal pellet groups that species are found in	Habitat type	Diaspore morphology	Seed length
Forb							
Asteraceae	Artemisia princeps		2	1	meadow and	no special	1.29 (M)
	I I I I				shrubland	morphology	
	Erigeron annuus	*	8	2	meadow and	wind	1.005
	0				shrubland		(M)
Brassicaceae	Capsella bursa-pastoris	*	1	1	meadow and	no special	0.95 (S)
					shrubland	morphology	
Caryophyllaceae	Cerastium glomeratum		1	1	meadow and	no special	0.4 (S)
					shrubland	morphology	
	Sagina japonica		1	1	meadow and	no special	0.345
					shrubland	morphology	(S)
	Stellaria aquatica	*	6	2	meadow and	no special	0.86 (S)
					shrubland	morphology	
Chenopodiaceae	Chenopodium album	*	26	6	meadow and	no special	1 (M)
					shrubland	morphology	
Lamiaceae	Clinopodium chinense var.		1	1	meadow and	no special	0.81 (S)
	shibetchense				shrubland	morphology	
Plantaginaceae	Plantago asiatica		5	3	meadow and	no special	2.025
					shrubland	morphology	(L)
Polygonaceae	Polygonum posumbu		1	1	meadow and	no special	
					shrubland	morphology	
Portulacaceae	Portulaca oleracea	*	13	4	meadow and	no special	0.665
					shrubland	morphology	(S)
Scrophulariaceae	Lindernia dubia	*	3	1	meadow and	no special	0.2 (S)
					shrubland	morphology	
	Mazus pumilus	*	1	1	meadow and	no special	0.3 (S)
					shrubland	morphology	
Solanaceae	Solanum americanum	*	13	4	meadow and	fleshy/edible	1.5 (M)
					shrubland	fruit	
Urticaceae	Pilea japonica		2	2	meadow and	no special	1.065
and denotified directions		0	0	shrubland	morphology	(M)	
unidentified dicot spp.		2	2				
Graminoid	C		1	1			
Cyperaceae	Cyperaceae sp.		1	1	hao wohoow		1 47 (14)
Poaceae	Agrosus cluvala var.		3	1	ineadow and	no special	1.47 (101)
	nukubo		1	1	sili ubialid	norphology	07(8)
	Daciyloclenium degyptium		1	1	chrubland	no special	0.7 (3)
	Digitaria ciliaria	*	10	11	sili ubialid	norphology	2 21 (1)
	Digitaria cuitaris		12	11	shrubland	morphology	3.21 (L)
	Panicum bisulcatum	*	4	2	meadow and	no special	177 (M)
	1 unicum Disticutum		7	2	shrubland	morphology	1.77 (101)
	Panicum dichotomiflorum	*	1	1	meadow and	no special	22(1)
	1 unicum ucholomijiorum		1	1	shrubland	morphology	2.2 (1)
	Poaceae sn		1	1	anabidilu	morphology	
Woody	i ouccae op.		1	-			
Actinidiaceae	Actinidia arguta		5	5	forest	fleshv/edible	2.38(1)
			~	~	101030	fruit	2.00 (1)
Salicaceae	Populus alba	*	1	1	cultivated	no special	1.5 (M)
	*				species	morphology	



Fig. 2. Comparison of plant species traits from regional flora and dispersed seeds in the feces. The CCZ (lowland area) flora indicates the available flora of CCZ and CCZ feces indicate the dispersed seed in the feces of CCZ (Lee and Lee, 2020). The TRF (forested area) flora indicates the available flora of TRF, while the TRF feces indicate the dispersed seed in the feces of TRF (this study). (A) growth form; (B) habitat type; (C) seed length; (D) diaspore morphology (**, P < 0.001; *, P < 0.05; NS, not significant; Fisher's exact test).

(Fig. 2A; P < 0.05; Fisher's exact test). From the vegetation data of the TRF, woody species accounted for approximately 70% and forbs approximately 25% of all species. In contrast, the proportion that germinated from feces largely consisted of forbs (68.2%), with woody plant growth forms only accounting for two species (9.1%).

In case of habitat type, species composition between the flora and deer feces differed significantly (Fig. 2B; P < 0.05; Fisher's exact test). The species originating from deer feces mostly originated from meadows and shrubland (90.9%). The species from flora was mostly comprised of forest species (79.2%), followed by meadow and shrubland species (16.8%).

The seed length category composition also differed according to species origin (Fig. 2C; P < 0.05; Fisher's exact test). From vegetation data, the species composition regarding seed length comprised 83.7% large (> 2 mm) seeds, but for species from the fecal pellet groups, the small (<1 mm) seeds were most abundant (42.9%), followed by medium (1–2 mm) seeds (38.1%).

Lastly, the proportion of species according to diaspore morphology also differed (Fig. 2D; P < 0.05; Fisher's exact test). From the vegetation survey, the species mostly consisted of fleshy or edible fruit (55.8%), followed by species with no special morphology (18.9%) and species adapted to wind dispersal (17.9%). In contrast, the species from fecal samples mainly consisted of species with no special morphology (90.9%).

Additionally, we compared the composition of the species traits with those of our previous study in the lowland areas (CCZ). For all traits tested, the species trait composition of regional flora in CCZ, and in TRF, were significantly different (Fig. 2; P < 0.05; Fisher's exact test). However, except for the habitat, the species composition of dispersed seeds in the CCZ and TRF showed no differences (P > 0.05; Fisher's exact test). The functional traits of species mainly found in feces were forbs, ≤ 2 mm seed length and showed no special morphology. For the habitat, the species composition of dispersed seeds in the CCZ and TRF were significantly different (Fig. 2B; P < 0.05; Fisher's exact test). Unlike the TRF feces, the CCZ feces had species from wet meadows (Fig. 2B).

4. Discussion

Through the seedling emergence method, we investigated potential endozoochory by Korean water deer in the Taehwa Research Forest, South Korea. Overall, the main functional traits of the species dispersed via endozoochory are forbs, with small seeds ≤ 2 mm,

S.-K. Lee et al.

from open habitats such as meadows and shrublands. Additionally, plant seeds had no morphological adaptation to specific modes of dispersal. These trends for species traits found from the feces were consistent with those found in our previous endozoochory study conducted in lowland areas, which has mixed landscape of wetlands, low forest hills, and arable lands (Lee and Lee, 2020).

Overall, we identified 115 seedlings and 22 species from 202 fecal pellet groups. Among the 22 species identified, 13 were consistent with a former endozoochory study in a lowland area (Table 1) (Lee and Lee, 2020). The most common species found in the fecal pellet groups of Korean water deer were *Chenopodium album*, *Portulaca oleracea*, and *Solanum americanum*. These species were also abundant in the feces of the Korean water deer in lowland areas (Lee and Lee, 2020). *Chenopodium album* is often found in the feces of ungulates in forest habitats (e.g., red deer and white-tailed deer) (Williams et al., 2008; Picard et al., 2016).

No seasonal differences in species and seeds dispersed by endozoochory were found. Additionally, unlike our former study on Korean water deer endozoochory conducted in CCZ, the proportion of the fecal pellet groups with at least one germinable seed was 19.8%, lower than that found in our previous study (54.8%) (Lee and Lee, 2020). We assume that this phenomenon is due to deer diet selectivity, as Korean water deer consume more forbs and graminoids when feeding in lowland areas (Kim et al., 2011, 2021). Dispersal of forb and graminoid seeds is more likely compared to that of woody plants, thereby, possibly reflecting in the increased consumption of forbs and graminoids in lowland areas as observed in our results.

The species that germinated in the fecal pellet groups were mainly forbs, with a seed length of ≤ 2 mm, from meadows and shrublands with no special adaptation to dispersal, consistent with a previous endozoochory study in the CCZ by Lee and Lee (2020). For the diaspore type, the species with no special dispersal adaptation were mainly dispersed through endozoochory, supporting the hypothesis proposed by Janzen (1984) that the seeds are unintentionally eaten while herbivores feed on the leaves of the plants and then subsequently dispersed. The seeds of open-area species have often been found in the ungulate feeces (e.g., Myers et al., 2004). Most deer species tend to feed in open habitat, and rest under forest cover (Kuijper et al., 2009). This might explain the occurrence of open area species found in the fees (Picard et al., 2016).

However, for habitats, the composition of species differed between the CCZ and TRF. More species from wetlands were dispersed in the lowlands than in forest habitats. As the lowland area of the previous study includes wetlands (Lee and Lee, 2020), the differences in flora between each region have affected the species compositions of species found in the feces. However, this phenomenon will be only possible if the seeds are able to survive in the gut.

Species with a seed length of ≤ 2 mm are mainly dispersed. Small seeds are more likely to escape the mastication and rumination of ungulates, as expected from previous studies (Couvreur et al., 2005; Pakeman et al., 2002). In addition, these species are likely to pass through the gut with less damage to the seed coat (Kuiters and Huiskes, 2010; Mouissie et al., 2005). According to the seed dormancy form, gut passage can either increase or decrease seed germination rate (Soltani et al., 2018). For physically dormant seeds, seed dormancy is broken and germination rate increases (Jaganathan et al., 2016). However, large and non-dormant seeds are broken, digested, and defecated in feces, whereas soft seeds are completely digested (Lee et al., 2021; Wang et al., 2017).

In our previous feeding experiments of Korean water deer (Lee et al., 2021), the overall gut passage had no significant effect on the germination rate of small, hard-coated seeds of *Amarantus magostanus*, *Chenopodium album*, and *Portulaca oleracea*. However, for *Panicum bisulcatum* seeds, which are probably soft-coated or non-dormant, a significant decrease in the germination rate was found (Lee et al., 2021). Thus, in addition to vegetation and vector diet, further investigation is required of seed dormancy form to comprehensively understand the endozoochoric processes regarding the consistent filter role of plant species.

Irrespective of plant composition in local flora, Korean water deer have the potential to disperse plant seeds of ≤ 2 mm in length from open habitats of forbs and graminoids, with no specific dispersal adaptation. This finding suggests that, even with differences in vegetation and plant availability, seed dispersal through gut passage and defecation plays a distinctive role in the ecological filtering plant species located where ungulates feed (Albert et al., 2015). Based on these findings, we suggest that by dispersing seeds with specific traits through endozoochory, Korean water deer endozoochory can act as a consistent ecological filter for plant species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

We attached data as supplementary data.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02325.

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