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Effects of Korean water deer (*Hydropotes inermis argyropus*) feces on seed germination and early seedling growth: insights into their contribution to seed dispersal

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Abstract

Endozoochory, the dispersal of seeds through the animal gut passage, plays a significant role in vegetation dynamics. The success of endozoochorous seed dispersal depends on each stage of the process: ingestion by animals, gut passage, and post-dispersal events after defecation. After the deposition of seeds through feces, the effects of feces on the initial stages of seedling establishment, including seed germination and seedling growth, can significantly impact overall survival. The pattern of fecal effects on plant species depends on the animal species. In this study, we investigated the effects of feces presence on seed germination and early seedling growth using feces of the Korean water deer (*Hydropotes inermis argyropus*). We conducted a germination experiment on 12 plant species belonging to 10 plant families, which are known to germinate in the feces of Korean water deer. The study compared the seed germination rate and seedling length after germination between seeds sown with and without feces of the Korean water deer. In general, we found that the presence of deer feces *per se* had no significant effects on seed germination and early growth stages. However, additional research on post-dispersal events such as long-term growth, fecal type, and germination conditions is needed to fully understand the costs and benefits of endozoochory.

Introduction

Endozoochory, the dispersal of seeds through the gut passage of animals, facilitates the dispersal of seeds from numerous plant species, facilitating the colonization in new habitats, and the expansion of plant populations (McConkey et al., 2012; Baltzinger et al., 2019). The success of the seed dispersal mechanism is influenced by various factors at each stage of the dispersal process (Cain et al., 2000; Baltzinger et al., 2019). In each stage of seed dispersal (i.e., from emigration, transfer, and to immigration), seed dispersal vectors contribute to plant dispersal in terms of both quantity and quality components (Schupp, 1993; van Leeuwen et al., 2022). Seed dispersal effectiveness depends on the quantity of seeds dispersed by animals and whether these seeds can germinate and establish in new habitats (Schupp et al., 2010). For endozoochory by ungulates, seed dispersal effectiveness has been widely examined in each stage, from ingestion of seeds, transportation of seeds through the animal gut, and to the dissemination stage (Baltzinger et al., 2019).

During the dissemination stage, seeds deposited through endozoochory encounter diverse environmental conditions (i.e., deposit quality) that significantly impact their survival and establishment (Baltzinger et al., 2019). These conditions include moisture level changes following the fecal desiccation, fecal types, feeding regime of animals, nutrient availability and seedling competition within fecal deposits (e.g., Milotić and Hoffmann, 2016b, 2017; Baltzinger et al., 2019; Karimi et al., 2020). Animal feces can serve as potential nutrient source containing elements such as nitrogen and potassium (Sakadevan et al., 1993; Williams and Haynes, 1995; Dai, 2000). Simultaneously, animal feces may contain harmful compounds that prevent seed germination (Marambe et al., 1993; Meyer and Witmer, 1998). The effects of fecal matter on seed germination and plant growth vary depending on the specific plant and animal species involved due to their fecal morphological types and digestion (Milotić and Hoffmann, 2016b; Guevara-Torres and Facelli, 2023; Ramos et al., 2024). These vector animal species-specific results emphasize the need of testing the response to each factor, which affects the successful results of endozoochorous seed dispersal. Understanding these effects is crucial for comprehending the dynamics of endozoochorous seed dispersal and early seedling establishment.

Hydropotes inermis argyropus, commonly known as the Korean water deer, is the most prevalent ungulate species on the Korean peninsula. This deer play a significant role in the dispersal of various plant species, especially forbs and those originating from open habitats

(Lee et al., 2021, 2022). A study by Park and Lee (2014) examined the influence of Korean water deer feces on the soil condition and growth of *Zea mays* seedlings. The authors found that the amount of feces added significantly affected the growth of *Zea mays* seedlings in nutrient-poor soil. This finding suggests that the fecal components of the deer can provide nutrients to the soil for plants to grow. However, at the same time, animal feces may also contain phytotoxic elements that could impede seed germination (e.g., frugivorous birds, Meyer and Witmer (1998); cattle and horse, (Milotić and Hoffmann, 2016b, 2017); cattle, chicken and pig, Marambe et al. (1993)), and still little is known about how the presence of the Korean water deer feces affects the germination and growth of plant species dispersed through the deer endozoochory. Given the relevance of endozoochory, it is imperative to systematically investigate and analyze the specific effects of feces on seed germination within this ecological context.

The objective of this study was to assess the effects of feces itself on seed germination and the early growth of seeds dispersed by the Korean water deer endozoochory through germination tests. Specifically, we investigated whether the presence of feces have an effect on (i) seed germination of species known to be dispersed through endozoochory and (ii) on the early growth of seedlings of 12 plant species previously reported to germinate from the feces of Korean water deer (Lee and Lee, 2020; Lee et al., 2022).

Materials and methods

Seed preparation

Based on previous studies (Lee and Lee, 2020; Lee et al., 2022), we selected 12 plant species that have been observed to germinate from the feces of the Korean water deer (Table 1). These species had previously been observed to germinate from the feces of the Korean water deer. The seeds of selected plant species were obtained for research purposes from the National Institute of Biological Resources. For species nomenclature, we followed a database managed by the National Institute of Biological Resources (https://species.nibr.go.kr/) and to determine whether each target species was an alien plant in South Korea, we referred to Korea National Arboretum (2019).

Table 1. The list of plant species tested for germination, and their growth form

Species		Growth form	Note
Amaranthaceae	*Amaranthus lividus*	Forb	
Asteraceae	*Erigeron annuus*	Forb	Alien plant
Brassicaceae	*Rorippa palustris*	Forb	
Caryophyllaceae	*Stellaria aquatica*	Forb	
Chenopodiaceae	*Chenopodium album* var. *centrorubrum*	Forb	Alien plant
Moraceae	*Morus bombycis*	Woody plant	
Onagraceae	*Ludwigia epilobioides*	Forb	
Plantaginaceae	*Plantago asiatica*	Forb	
Poaceae	*Panicum bisulcatum*	Graminoid	
	Digitaria sanguinalis	Graminoid	
Urticaceae	*Urtica angustifolia*	Forb	
	Pilea mongolica	Forb	

The species that are categorized as alien plants are followed by Korea National Arboretum (2019).

Feces preparation

For the experiments, the feces of the Korean water deer were collected from Taehwa Research Forest and Civilian Control Zone, where previous sampling had been conducted (Lee and Lee, 2020; Lee, et al. 2022). The fecal pellet groups were individually stored in zipper bags, transported to the laboratory, and cleaned on their outer surface. Subsequently, the fecal pellets were allowed to air-dry at room temperature. To mitigate the potential effects of different sampling seasons and sites, all collected fecal samples were combined. The feces were ground to avoid possible contamination from external seeds and to ensure a consistent fecal amount could be used in the experiments.

Experimental setup

For the experimental setup, above mentioned 12 plant species were tested for germination under conditions of with (feces) and without the feces (control) of the Korean water deer. For each species, five seeds were sown in each pot, resulting in 10 replications for each treatment (with and without feces), and thus a total of 240 pots were tested. The pots (150 mm in diameter and 135 mm in height) were filled with commercial soil (Baroker, Seoul Bio Co., Ltd., Eumseong, Korea). In each pot with the treatment condition of adding the feces of Korean water deer, 5 g of air-dried and ground feces was added. All seeds were directly sown on the surface of feces or soil to facilitate light availability. The experiment was carried out at the temperature-controlled greenhouse facility at Seoul National University. The temperature of the greenhouse was set at 23°C during the experiments. The pots were watered on a regular basis and kept moist. During the experimental period, the pots were randomly allocated and redistributed every other day. The number of seedlings that germinated for each species (emergence rate) in each treatment was checked 60 days after the initial day of sowing, and the height of each seedling was measured.

Data analysis

To investigate the effects of fecal presence on the seedling emergence rate in each species, a Generalized Linear Model (GLM) of Poisson distribution was applied. To compare the effects of fecal presence on seedling height, the data were validated for homogeneity and homoscedasticity prior to analysis, and the *t*-test and Wilcoxon rank-sum tests were used. Visualization of the data was conducted using ggplot2 (Wickham, 2016) package. All analyses were conducted in R version 4.2.1 (R Core Team, 2022).

Results

Number of seedlings emerged

All 12 tested plant species germinated. Across all treatments (control and feces) and species, a median of one seed germinated per pot sown with five seeds. For all 12 species tested, the comparison of the seeds that were sown on the feces had no significantly different emergence rate from that of seeds that were sown in soil ($P > 0.05$; GLM model fitted with Poisson distribution; Fig. 1). The results showed that overall, the feces had no

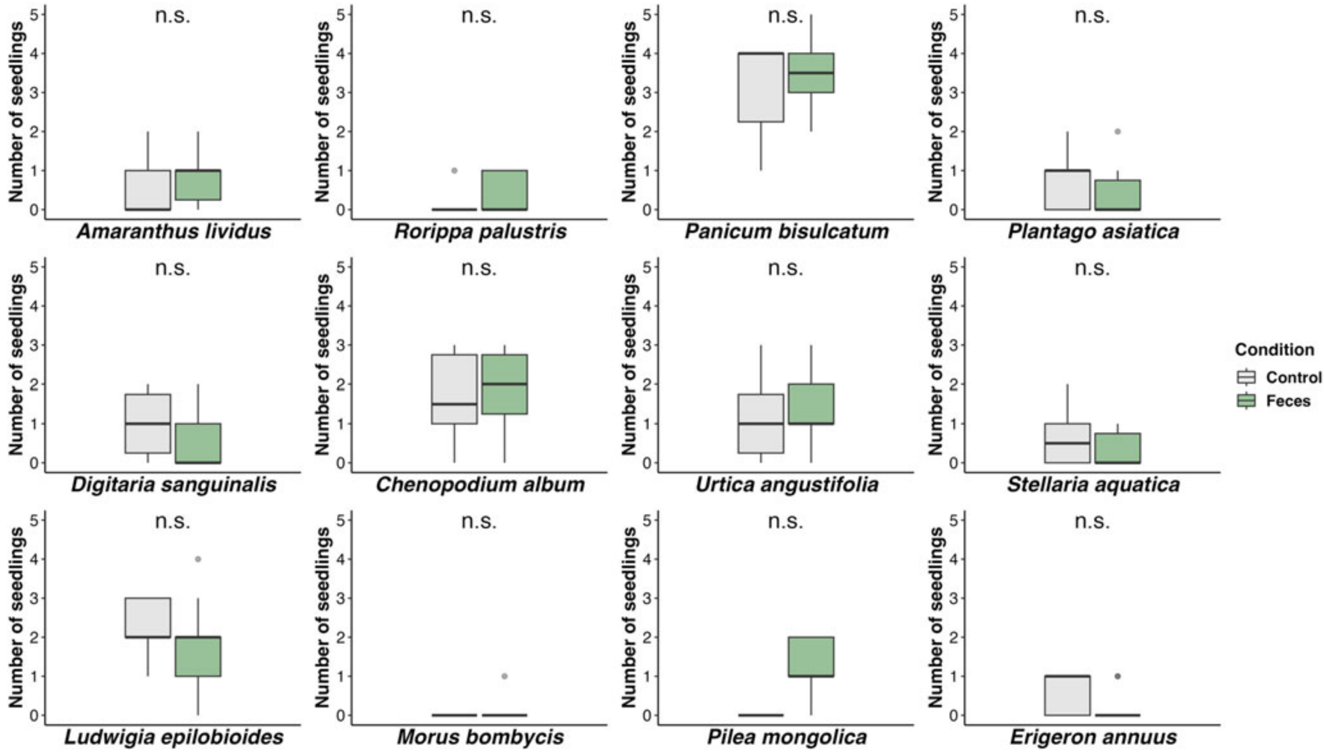

Figure 1. The number of seedlings of each plant species germinated in a condition with feces (Feces) and without feces (Control) of the Korean water deer. n.s. denotes for not significant ($P > 0.05$) based on the GLM model with Poisson distribution.

significant impact on the germination rate of any species. Detailed statistics can be found in the Supplementary Table 1.

Seedling height

On the final day of the germination test, we measured the height of each seedling that germinated. We found that the height of all species that germinated showed no differences from that of control seedlings that were sown on the soil for 11 out of 12 plant species tested ($P > 0.05$; *t*-test; Fig. 2; Supplementary Table 2). In the case of *Urtica angustifolia* sown on the ground feces showed higher seedling height compared to that of the control condition (*t*-statistic = 2.657; d.f. = 12.138, $P = 0.021$; *t*-test).

Discussion

Understanding the effects of feces on seed germination and seedling growth enables us to comprehend the costs and benefits associated with the entire process of endozoochorous seed dispersal. This study aimed to investigate the influence of Korean water deer feces itself on seed germination and initial seedling growth of plant species dispersed through Korean water deer endozoochory. Among the 12 species studied, there were no significant differences in seed performance between those sown with feces and those sown without feces, and no differences in seedling growth for 11 of these species, except for *U. angustifolia*. Our findings indicate that negligible impact of feces *per se* on seed germination and initial seedling growth in the context of the Korean water deer endozoochory.

Previous studies suggest that the response of plant species depends on the plant species and physiology of animal species involved (e.g., ruminant and hindgut-fermenting). The results of this study could be associated with the gastrointestinal physiology of Korean water deer, a ruminant species. While the effects of feces on seed germination differed among plant species, certain species exhibited lower germination rates when exposed to feces (Milotić and Hoffmann, 2016b). These results are also affected by the fermented gut characteristics of cows and horses (Milotić and Hoffmann, 2016b). Additionally, in a study examining *Neltuma flexuosa* seed germination and seedling growth with feces from cow, horse and mara, the results varied depending on the animal species (Ramos et al., 2024). Horse and mara feces showed reduced germination rates, while cow feces had no discernible effects. Regarding seedling growth, the native and wild mara species showed negligible effects, whereas domestic cow and horse species exhibited increased seedling growth compared to normal conditions. Moreover, the effects of native herbivore kangaroo and domestic sheep on different plant species also varied, promoting the growth of aboveground biomass in wallaby grass and reducing wild oat aboveground biomass, depending on the animal species involved (Guevara-Torres and Facelli, 2023). Therefore, it is essential to analyze and compare the results specific to both animal and plant species, to understand the ecological correlation between seed dispersal through endozoochory and associated animals and plants. Furthermore, it is crucial to consider not only the seed germination rate but also the timing of seed germination. Previous research has shown that feces can delay seed germination (Meyer and Florence, 1996; Ramos Font et al., 2015; Milotić and Hoffmann, 2016b). Additionally, certain species exhibited low germination rates, suggesting that their germination requirements may not have been met, including mortality shortly after germination. For example, *Morus bombycis* showed a particularly low germination rate.

Overall seedling height showed no significant differences with the addition of feces. However, for *U. angustifolia*, the addition of

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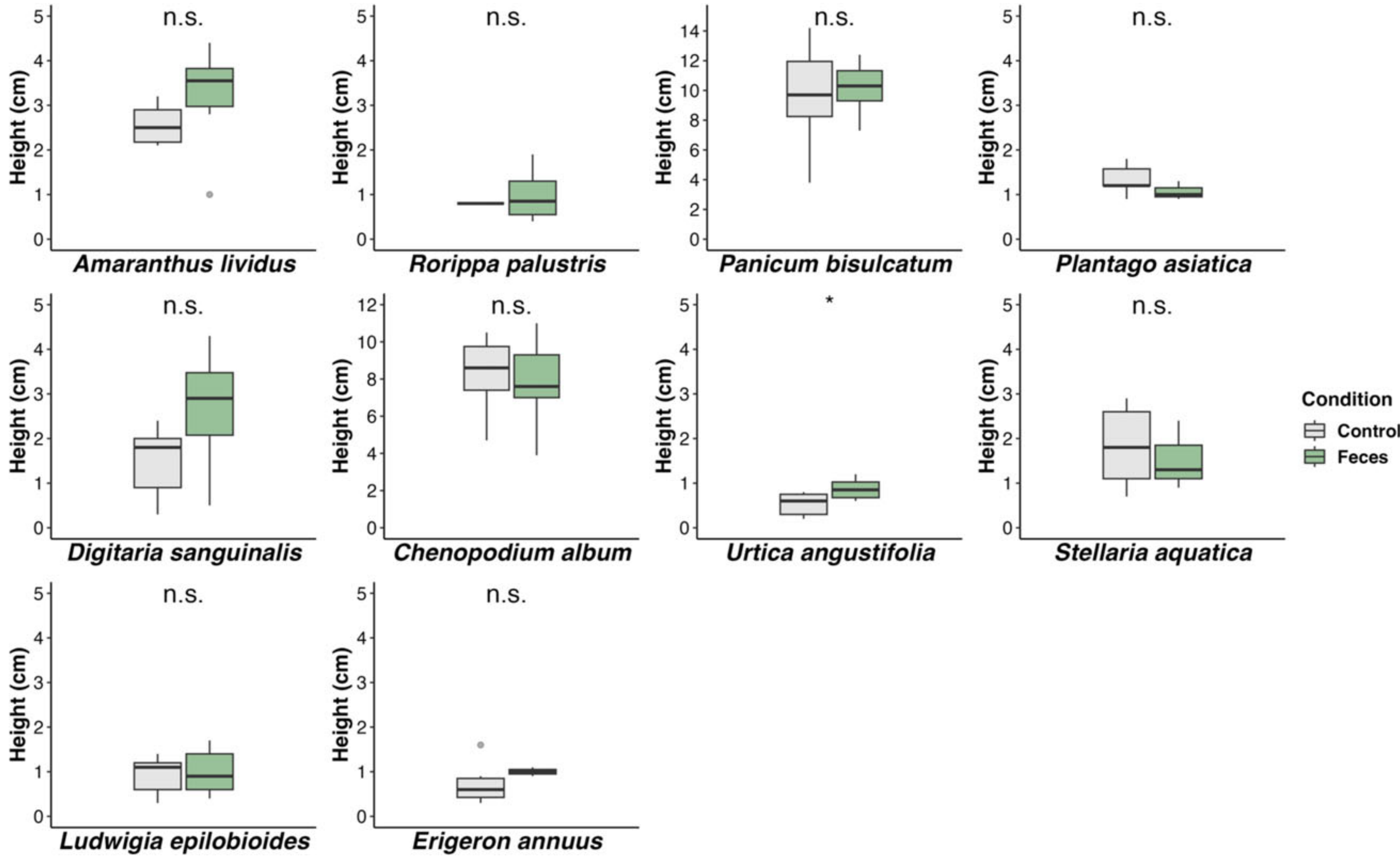

Figure 2. Seedling height of each plant species germinated in a condition with feces (Feces) and without feces (Control) of the Korean water deer. n.s. denotes for not significant and * denotes for significant ($P < 0.05$) following the *t*-test.

feces showed higher growth (Fig. 2). It is important to note that the low germination rate for some species could have obscured the results, which could reduce the statistical power. In our study, we only assessed the early growth of the seedlings, which did not allow for the evaluation of the longer-term effects of feces on seeds of species dispersed through endozoochory. However, a study by Milotić and Hoffmann (2016a) demonstrated that over an extended growth period, plants with feces showed higher biomass production compared to those without feces. Related to this, Park and Lee (2014) tested the effects of the Korean water deer feces on the growth of *Zea mays*, demonstrating that the addition of feces resulted in greater plant material production than in plants without feces in nutrient-poor soil. Although we found negligible effects on early seedling stages, seed dispersal through the Korean water deer endozoochory may have positive consequences by promoting the growth of plant species in the longer term, as the fecal components can release the potential beneficial nutritions such as nitrogen, potassium, phosphorus (Rowarth et al., 1985; McDowell, 2006; Park and Lee, 2014; Park et al., 2015). Moreover, this pattern could also be related to the time it takes for nutrients to be released from fecal materials through physical breakdown and mineralization processes (Rowarth et al., 1985; Eichberg et al., 2007).

According to our previous feeding experiments of the Korean water deer, testing the effects of gut passage on seed germination, the seeds consumed by water deer exhibited a recovery rate of less than 30% across all tested species (Lee et al., 2021). It is evident that a considerable proportion of seeds undergo consumption during gut passage, which can be related to the seed traits including seed morphology (Mouissie et al., 2005; Lee et al., 2021). The low recovery rate of ingested plant seeds, combined with potential seedling competition, could significantly impact the overall survival and dispersal success of seeds through endozoochory. Based on the current results and our former research on gut passage effects (Lee et al., 2021), the deer is not an effective endozoochorous seed disperser. According to a meta-analysis study (Torres et al., 2020), the deer family (Cervidae) is not an effective seed dispersal vector for endozoochory, showing that gut passage by deers has no significant effects on seed germination. Furthermore, despite our efforts to assess the impact of Korean water deer feces on seed germination and seedling growth, a thorough experimental design using gut-passed seeds is essential to evaluate the effectiveness of endozoochorous seed dispersal, as the gut passage may alter the chemical and mechanical aspects of seeds (Samuels and Levey, 2005).

Endozoochorous seed dispersal is a comprehensive process, involving ingestion, defecation, and post-dispersal events. As the overall success of emergence and fruiting in real situations has low probabilities (Eichberg et al., 2007), final seedling emergence in real deposition events and fruiting stage also needs to be tested. After deposition, the feces are likely to undergo changes in their nutritional components and moisture (Holter, 1991, 2016). Moreover, we placed the seeds on the top parts of ground feces; however, in real deposition events, the water deer defecate the seeds in the structure of small fecal pellet groups, which may impose additional physical and biological barriers to seed germination. The feces type of deer is usually fecal pellet groups defecated with several small fecal pellets and is prone to desiccate after deposition (Welch, 1985; Eichberg, et al. 2007; Milotić and Hoffmann, 2016b), affecting seed germination due to moisture loss.

After deposition through endozoochory, seeds encounter not only environmental factors such as habitat deposition site, weather, and moisture (Dickinson and Craig, 1990), but also, biological components including secondary seed removal by dung beetles (Milotić et al., 2019; Urrea-Galeano et al., 2019) and seedling competitions (Milotić and Hoffmann, 2017), and each stage determining the success of endozoochorous seed dispersal. Furthermore, in outdoor environments, the seed germination rate would be decreased due to the fast desiccation in the outdoor environments, and the germination conditions in the outdoor environments compared to greenhouse results in a lower germination rate as well (Milotić and Hoffmann, 2016b; Karimi et al., 2020). Furthermore, we sowed five seeds to avoid possible intra-species competition; however, in our former Korean water deer results, the highest density showed 161 seedlings per fecal pellet group (Lee and Lee, 2020), suggesting possible higher competition among seedlings. Intra-species competition may have different effects on seedling dispersal patterns as well (Milotić and Hoffmann, 2017). Therefore, the comprehensive understanding of endozoochorous seed dispersal processes by the Korean water deer needs to be thoroughly investigated from ingestion to defecation to comprehensively understand the costs, benefits, and overall effectiveness.

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