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Owl-mediated diploendozoochorous seed dispersal increases dispersal distance and supports seedling establishment

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ABSTRACT

Seed dispersal is an essential process contributing to the maintenance of plant populations. Zoochory is a widespread way of plant dispersal in every terrestrial ecosystem that can ensure the long-distance dispersal of seeds. Secondary seed dispersal (SSD) by far-ranging raptors is a special type of zoochory, which might have a role in colonizing new habitats. We used the barn owl (*Tyto alba*) as model species to test the effectivity and seasonality of SSD in open semi-natural landscapes. We collected 582 pellets from six sites in East-Hungary throughout one year. We identified prey items in the pellets and determined the viable seed content of the pellets by germination experiments. We found that herbivorous *Microtus arvalis* L. was the most abundant prey item through which most of the seeds spread. Owls dispersed the seeds of generalist and disturbance-tolerant plants, indicating the habitat type where small mammals occur abundantly. In another experiment we tested the effect of the pellet material on the seedling survival and found that prey remains enhanced establishment of seedlings. Our study suggests that SSD by barn owl is occasional but important event in long-distance seed dispersal. Since the studied owl species uses several habitat types and has larger mobility than the rodents, the revealed dispersal mechanism can considerably increase seed dispersal distance and seed exchange between habitat types.

1. Introduction

Since adult individuals of plant species have limited mobility, their spatial movement is generally realised by the dispersal of their seeds (Nathan, 2006). Seed dispersal is essential to ensure regional persistence of the populations, to reduce the risk of local extinctions, and to enhance re-establishment by recolonization. Thus, it determines the distribution, abundance, and population structure of plants (Hanski, 1999; Lindborg et al., 2012). Ongoing climate change, accelerating loss and fragmentation of natural habitats are further increasing the importance of dispersal processes that can maintain functional connections among metapopulations and by that the functioning of ecosystems (Chen et al., 2011; Fletcher et al., 2018; Godó et al., 2022). Good dispersal ability makes plants less sensitive to negative environmental changes such as shifts in the climate, as they might be able to move between habitat patches with slightly different attributes (Auffret et al., 2015; Lepková et al., 2018).

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Zoochory – seed dispersal by animals – is one of the most widespread plant dispersal types in terrestrial ecosystems. As some animal species are able to travel long distances with seeds on their outside or seeds inside their guts, zoochory supports the long-distance dispersal of seeds (Nathan, 2006). However, the decline of the seed-dispersing large herbivores severely affecting the dispersal-driven ecosystem processes on a global scale (Burney and Flannery, 2005; Farwig and Berens, 2012; Kamp et al., 2016), and implies that alternative, often overlooked dispersal mechanisms and animal groups play a key role in seed dispersal interactions (Jansen et al., 2012; Pérez-Méndez and Rodríguez, 2018; Godó et al., 2022). Pérez-Méndez and Rodríguez (2018) stressed that literature about zoochorous seed dispersal was focused for a long time on the role of frugivorous mammals and birds. Also, in grasslands, studies predominantly focused on the role of large body-sized herbivores (Poschlod and WallisDeVries, 2002; Mouissie et al., 2005; Couvreur et al., 2008; Lepková et al., 2018).

Some recent studies aim to explore and highlight the importance of other dispersal vectors, such as rodents, carnivores and raptors (Godó et al., 2022; Jansen et al., 2012; Hämäläinen et al., 2017; Pérez-Méndez and Rodríguez, 2018). They pointed that many of the seeds located near the soil surface will likely be encountered and eaten, dispersed, or ignored by rodents as they are present wherever seeds are. Rodents can be both quantitatively and qualitatively efficient dispersers of many plant species, including those without evident specialization for endo- or epizoochory (Liebman et al., 2001; van Leeuwen et al., 2020; Jansen et al., 2012). The outcome of rodent-mediated seed dispersal and the array of dispersed seeds highly depend on the rodents' feeding strategy (herbivores, omnivores or carnivores). Due to the phenology of plants and seasonal changes in forage preferences of rodents the species composition of dispersed seeds might show a marked seasonality (Godó et al., 2022). By controlling the population density of rodents, raptors can considerably affect seed dispersal processes. Many raptor species are highly dependent on rodents which constitute a large proportion of their diet (Ferguson-Lees and David, 2001). This trophic connection implies the possibility of secondary seed dispersal (SSD). SSD happens when a seed is being dispersed in two or more steps by distinct dispersal agents. In the case of raptors, SSD generally occurs when a primary seed disperser or seed predator (e.g., a herbivorous or granivorous rodent) is caught and consumed in the foraging grounds or transported from there for consumption or deposition. Hence, the seeds which have been in contact with the rodent are relocated, which could happen with or without ingestion of the seeds. This divides SSD processes into three subtypes: diplotendoochory (seeds are ingested both by the rodent and raptor), diplotendosynzoochory (seeds are ingested by the rodent but not by the raptor) (Pérez-Méndez and Rodríguez, 2018) and diplosynendozoochory (seeds are not ingested by the rodent but ingested by the raptor) (Grant et al., 1975). Beyond their role in seed dispersal, vertebrate predators may influence germination rate (Padilla and Nogales, 2009; López-Darias and Nogales, 2016) and can support seedling establishment by providing nutrients via their excreta, such as pellets (Fedriani et al., 2015).

By now, the role of diurnal raptor species e.g., hen harrier (*Circus cyaneus*), common buzzard (*Buteo buteo*) and common kestrel (*Falco tinnunculus*), has been proved in seed dispersal (see in detail Hämäläinen et al., 2017; Pérez-Méndez and Rodríguez, 2018). Also, the presence of seeds in nocturnal raptors' (like owls) pellets are mentioned (Maser and Brodie, 1966; Grant et al., 1975; MacCracken et al., 1985; Álvarez-Castañeda et al., 2004; Shehab and Al Charabi, 2006), but the outcome of this phenomenon has rarely been tested by germination experiments (but see Dean and Milton, 1988; Pearson and Ortega, 2001). There are differences between SSD effectivity of diurnal and nocturnal raptors which is a consequence of their feeding behaviour. Most diurnal raptors remove their prey's digestive tracts before consumption (so presumably most of the seeds consumed by the prey as well), then the body of the prey is eaten piece by piece. In contrast owls often swallow their prey in whole (König and Weick, 2008), which implies that seeds not yet digested by rodents are swallowed and may remain intact. Both groups regurgitate the preys' undigested parts (such as bones, feathers, and hair) in the form of pellets. Formation of pellets take up several hours which predicts the retention of consumed seeds in the stomach of the raptor. This may further increase seed dispersal distance by raptors during their daily movements, vagrancy, or migration (Hämäläinen et al., 2017).

In the perspective of alternative dispersal agents, research on open habitats is still apparently overlooked, especially if compared to woody habitats (Pearson and Ortega, 2001; Gómez et al., 2019; Godó et al., 2022). To decrease this knowledge gap, here we studied a three-level dispersal network consisting of seeds, rodents and nocturnal birds of prey in open landscapes. We tested i) whether SSD by barn owls (*Tyto alba*) that are widespread nocturnal predators is present in open landscapes, ii) the effects of seasonality on the number of species and seeds dispersed by SSD, and iii) whether the presence of pellets have an effect on germination and seedling establishment.

2. Material and method

2.1. Study area and model species

Our study area is located in the Hortobágy National Park, Great Hungarian Plain, East Hungary (Fig. 1). The region is characterized by a continental climate with a mean annual precipitation of 550 mm and a mean annual temperature of 9.5 °C with high interannual fluctuations (Fick and Hijmans, 2017). The elevation ranges between 88 and 102 m a.s.l. The study area is characterized by vast stands of open habitats such as alkaline and loess grasslands, wetlands, and alkaline marshes and some agricultural fields in the periphery of the protected areas (Deák et al., 2014).

As model species, we chose a nocturnal raptor, the barn owl, as this bird is widespread and common across Europe's farmlands (König and Weick, 2008) and as a cosmopolitan species it occurs in all continents except Antarctica (BirdLife International, 2019). During daytime, barn owls most frequently roost in barns, attics of large buildings or church towers, but also use other terrain features such as trees and taller bushes. They regurgitate pellets containing undigested prey remains at roosts during daytime and during hunting, so generally two times a day (Ács, 1985). The blackish pellets of barn owls are covered by a silky gloss (film of saliva); thus,

are easy to distinguish from other birds' pellets (König and Weick, 2008). Barn owls have broad dietary range but bias their diet towards mammal species that are widely available as prey (Kiamos et al., 2019). They are not opportunistic feeders but prefer prey weighted between 5 and 30 g (König and Weick, 2008).

2.2. Sample collection

In 2019, we collected barn owl pellets from abandoned agricultural buildings from six locations where constantly present pairs of owls were reported (Fig. 1). From each location twenty-five pellets were collected in every season from spring to winter (four collection dates); except in autumn when from three locations, we could collect only 23, 21 and 13 pellets, respectively. In total we collected 582 pellets. Only fresh and intact pellets were collected. The pellets were checked for contamination with soil or attached propagules during collection and parts with soil contact were removed. The pellets then were placed in paper bags individually and were stored in cool and dry place until the beginning of the germination experiments. We also collected twenty-five additional pellets in spring from one of the locations where plenty of fresh pellets were available, for testing the effect of pellets on plant establishment.

2.3. Greenhouse experiments

2.3.1. Prey identification and germination experiment from pellets

Samples collected during spring and summer were processed after collection, in May (spring sample) and August (summer sample) 2019. Autumn and winter samples were processed in March 2020. Pellets were dissected individually. The prey item content of each pellet was determined by using the identification keys by Ujhelyi (1994). Based on their skull morphology, we identified every small mammal remain (voles, shrews and murids) to the species level if it was possible and every other taxon (such as orthopterans and bugs) to the order or family level, as these were not relevant to our study. For small mammals, we recorded the number of specimens per species for each pellet, which was based on the number of skulls in the pellet, as owls swallow their prey whole.

The germination experiments were performed in an unheated greenhouse from May 2019 to June 2020. Dissected pellets were placed independently in $8.5 \times 8.5 \times 8$ cm pots containing potting soil (standard planting substrate containing turf, humus and manure). Pots were marked individually. We also used control pots containing only potting soil, to be able to discriminate seeds

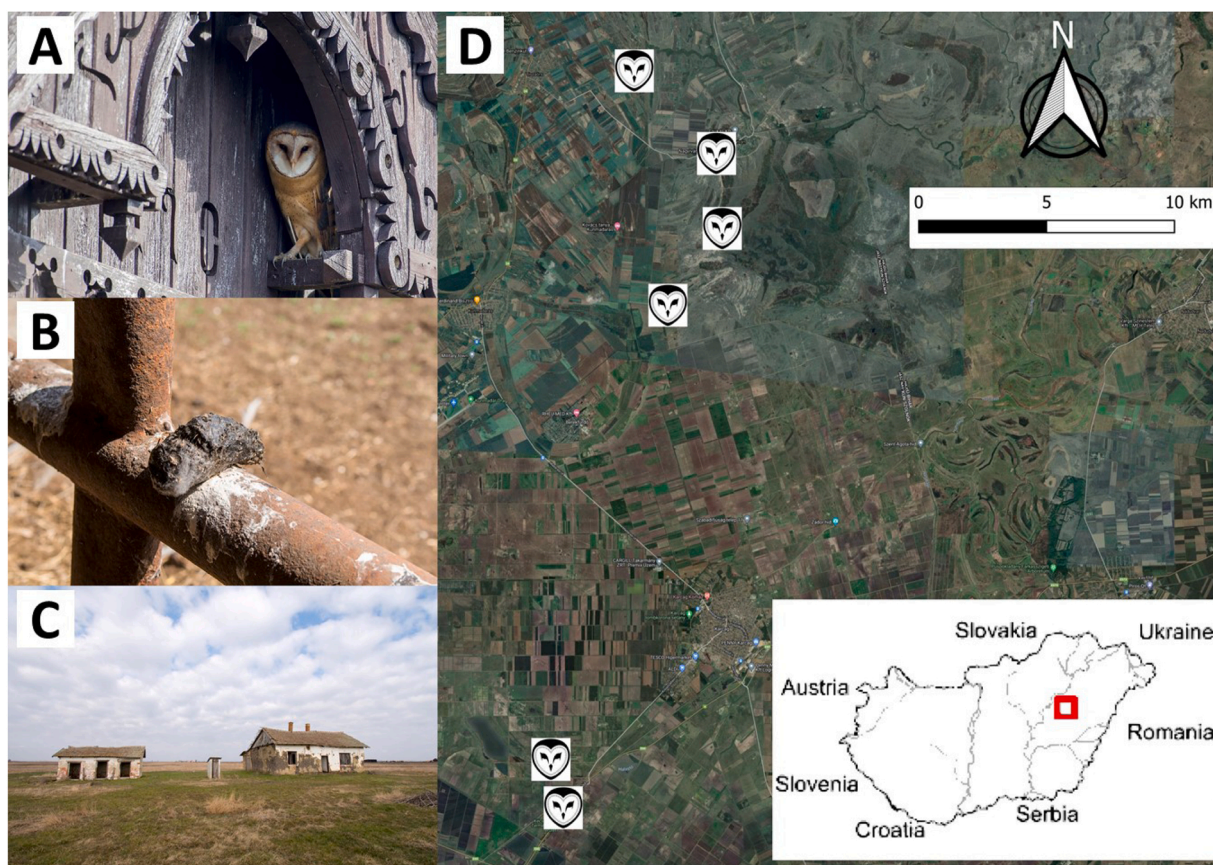


Fig. 1. A) Barn owl (*Tyto alba*); B) Barn owl pellet on barn's fence; C) Typical breeding and roosting place of barn owls in the study region; D) Location of the six sampling sites in East Hungary.

germinating from the substrate. Twenty-five control pots were made for each germination period, altogether 100 control pots were used. In total 18 seedlings of 5 species germinated from the control pots, of which each species germinated from the samples, too. These species were excluded from the analysis. Experimental and control pots were watered every day, and seed germination, defined as any seedling part having emerged above the soil surface, was noted every two days for three months. After the germination period seedlings that emerged above the soil surface were identified to species level if it was possible using Csapody (1968) and Király (2009) and then were removed.

2.3.2. Effect of pellet material on plant establishment

We used white mustard (*Sinapis alba*) seeds for this experiment as mustard seeds are easily available, easy to handle and are characterized by high germination synchrony, rapid establishment and growth. As mustard does not occur in wild and is not cultivated in the study region, we could assume that the pellets used for the experiment did not contain its seeds. In April 2019, mustard seeds were placed into 50 pots (25 seeds in each pot) containing potting soil. Dry pellets were broken apart and mixed in a bowl to create a homogeneous material. This homogeneous pellet material was spread out evenly with a thickness of 1 cm over the top of the sown seeds in 25 pots; the other 25 pots functioned as control (without pellet). Pots then were treated the same manner and were watered every day. Germination lasted for four weeks. After four weeks the seedlings in each pot were counted and removed. We measured the dry mass of the aboveground biomass of the seedlings in each pot with an accuracy of 0.0001 g.

2.4. Data processing

We assigned traits to the germinated plant species, such as thousand seed weight (TSW, Török et al., 2013), main dispersal strategy (MDS, Sádlo et al., 2018) and social behaviour type (SBT, Borhidi, 1995) (Table 2). MDS classification is based on that a single plant species usually uses not a single, but a combination of several dispersal modes. Repeatedly occurring combinations in different plant taxa are called dispersal strategies. Species are assigned to nine dispersal strategies named for the genus names of typical representatives, that is, Allium, Bidens, Cornus, Epilobium, Lycopodium, Phragmites, Sparganium, Wolffia, Zea (Sádlo et al., 2018). MDS traits were derived from the Pladias database (Chytrý et al., 2021). SBT classification is based on the model of Grime (1979), but was adapted for the Hungarian conditions and indicates the role of species in the plant communities. At the community level SBT can reflect stability, regeneration ability, naturalness and degree of disturbance. In the SBT classification species were assigned to six functional groups (competitors, generalists, natural pioneers, disturbance-tolerants, weeds and ruderal competitors) along a gradient from the species typical of natural habitats to the species typical of degraded habitats (Borhidi, 1995).

To test how seedling number is affected by season we fitted a Conway-Maxwell Poisson generalized linear regression model (GLM) which was described to handle under- and overdispersion well (Sellers and Premeaux, 2021). We used seedling number as response variable, and season as predictor. We also tested whether or not pellet treatment had any effect on the number of mustard seedlings (using zero-inflated Conway-Maxwell Poisson GLM), and total mass of seedlings. We used log-linked Gamma GLM (since we included observations where no seedlings emerged, we had to increment all values by 1 to be able to fit the Gamma model). One observation (pellet) from autumn with a sum of 30 seedlings, was excluded from this analysis as a singular extreme outlier. Five species which germinated both from the pellets and the control pots were excluded from the analysis.

Additionally, we tested how treatment affected average seedling mass (excluding observations with no germinable seeds), using log-linked Gamma GLM. We chose to use Gamma GLMs for the continuous data (total and average seed mass) because they exhibited substantially skewed distributions, which this model family can handle well. Between-group contrast estimates (e.g. autumn – spring) from the GLMs were acquired using the R-package “emmeans” which enables the post hoc estimation of estimated marginal means, trends, and contrast parameters (Lenth et al., 2018). All data handling and statistical data analyses were carried out in R (v. 4.1.2, R Core Team, 2021).

3. Results

3.1. Prey and seed content of the pellets

We recorded 1754 individuals of 13 small mammalian taxa in the pellets. The full list of the recorded species, and the detailed number of individuals are given in Table 1. The vast majority of the prey items was common vole (*Microtus arvalis*, 62.5 %) which was the most frequent in all seasons, especially in summer (Table 1).

The germinated plants from the pellets belonged to 14 families (Table 2, Appendix 1). Emerged species could be grouped into five categories according to their main dispersal strategy, that is, Allium-type (autochory) – 15 species, Bidens-type (autochory and epizoochory) – 1 species, Cornus-type (autochory and endozoochory) – 1 species, Epilobium-type (anemochory and autochory) – 3 species, Sparganium-type (autochory and hydrochory) – 2 species. Most of the germinated species were generalists and disturbance-tolerant plants typical to natural habitats (Table 2).

Five plant species with a total of 30 seedlings emerged from a single pellet collected in autumn (Table 2, Appendix 1). Not considering this outlying data, the total number of plant species emerged from the pellets was ten in spring, one in summer, four in autumn and three in winter (Table 2). We found that pellets collected in spring contained the most viable seeds (18 % of all pellets collected in spring contained germinable seeds, and 63 % of the germinated seedlings were originated from these samples) (Table 2, Fig. 2, Appendix 2, Appendix 3). Pellets collected in summer contained only one germinable seed. Pellets collected in winter and autumn contained an intermediate number of germinable seeds. In autumn, 7 % of all pellets collected contained germinable seeds,

Table 1

The full list of the recorded prey items and the number of individuals per season.

Species	Spring	Summer	Autumn	Winter	Σ
<i>Apodemus agrarius</i>	5	5	3	0	13
<i>Apodemus</i> spp. (<i>A. sylvaticus</i> , <i>A. flavicollis</i> , <i>A. uralensis</i>)	25	9	15	11	60
<i>Arvicola amphibius</i>	5	5	13	11	34
<i>Crocidura leucodon</i>	35	24	47	40	146
<i>Crocidura suaveolens</i>	32	7	13	17	69
<i>Micromys minutus</i>	9	1	0	1	11
<i>Microtus arvalis</i>	237	345	254	261	1097
<i>Microtus subterraneus</i>	0	0	0	1	1
<i>Mus</i> spp. (<i>M. musculus</i> , <i>M. spicilegus</i>)	14	16	25	8	63
<i>Neomys anomalus</i>	0	0	2	1	3
<i>Rattus</i> spp. (<i>R. rattus</i> , <i>R. norvegicus</i>)	1	3	0	2	6
<i>Sorex araneus</i>	62	31	30	29	152
<i>Sorex minutus</i>	34	29	20	16	99
Σ all	459	475	422	398	1754

Table 2List of the plant species germinated from pellets. Notations: MDS – Main Dispersal Strategy (Sádlo et al., 2018), SBT – Social Behaviour Type (Borhidi, 1995); * – species from the pellet with 30 germinated seedlings (*Convolvulus arvensis* occurred in two other cases).

Species	No. germinated seedlings	Season of collection	MDS	Thousand seed weight (g)	SBT
<i>Alopecurus geniculatus</i>	2	autumn	Sparganium	0.0883	generalist
Apiaceae sp.	1	spring	Allium	NA	NA
<i>Bolboschoenus maritimus</i>	1	winter	Sparganium	2.9640	competitor
<i>Carex</i> sp.*	1	autumn	Allium	NA	NA
<i>Chenopodium album</i>	5 + 4	autumn, winter	Allium	0.7580	ruderal competitor
<i>Coryza canadensis</i>	1	spring	Epilobium	0.0600	alien species
<i>Convolvulus arvensis</i> *	2 + 1*	spring, autumn	Allium	10.0507	ruderal competitor
<i>Dactylis glomerata</i>	9	spring	Allium	0.3460	disturbance tolerant
<i>Digitaria sanguinalis</i>	4	spring	Allium	0.6707	alien species
<i>Epilobium tetragonum</i>	1	spring	Epilobium	0.0507	generalist
<i>Fragaria viridis</i>	1	winter	Cornus	0.4890	generalist
<i>Hibiscus trionum</i>	1	spring	Allium	3.7860	ruderal competitor
<i>Lotus corniculatus</i> *	1	autumn	Allium	1.2607	disturbance tolerant
<i>Medicago lupulina</i>	3	spring	Allium	1.1333	disturbance tolerant
<i>Myosurus minimus</i>	1	summer	Allium	0.0737	natural pioneer
<i>Polygonum aviculare</i>	2	spring	Allium	1.8270	ruderal competitor
<i>Setaria verticillata</i>	5	spring	Bidens	1.1887	ruderal competitor
<i>Tamarix tetrandra</i>	1	autumn	Epilobium	~0.1000	alien species
<i>Trifolium striatum</i> *	9	autumn	Allium	2.1260	natural pioneer
<i>Urtica dioica</i>	1	autumn	Allium	0.1583	disturbance tolerant
<i>Vicia angustifolia</i> *	16	autumn	Allium	11.0943	disturbance tolerant
<i>Vicia hirsuta</i> *	2	autumn	Allium	3.4903	disturbance tolerant

and 22 % of the seedlings were originated from these samples. In winter, germinable seed were found in 3 % of the collected pellets, and 13 % of the total seedlings were derived from these samples. The maximum number of germinated seedlings was two per pellet both in spring, autumn, and winter and one per pellet in summer (Fig. 2).

3.2. Effect of pellet material on plant establishment

The presence of pellet material had a significant effect on the viability of seedlings. The number of seedlings recorded four weeks after seed sowing and the total and individual mass of seedlings were significantly higher in pots where seeds were covered with pellets (Fig. 3).

4. Discussion

Most recent research highlights the importance of overlooked vertebrate seed dispersers including raptors. Raptors may be involved in multi-level long-distance dispersal processes which can have a high impact on plant populations (López-Darías and Nogales, 2016; Pérez-Méndez and Rodríguez, 2018). In this study we tested a two-step seed dispersal system based on predation on rodents by barn owls in an open landscape. We found that pellets contained viable seeds and the number of germinated seedlings showed seasonality. Germinated plants were mostly early successional species connected to open habitats. We also found that prey remains had positive effect on plant establishment.

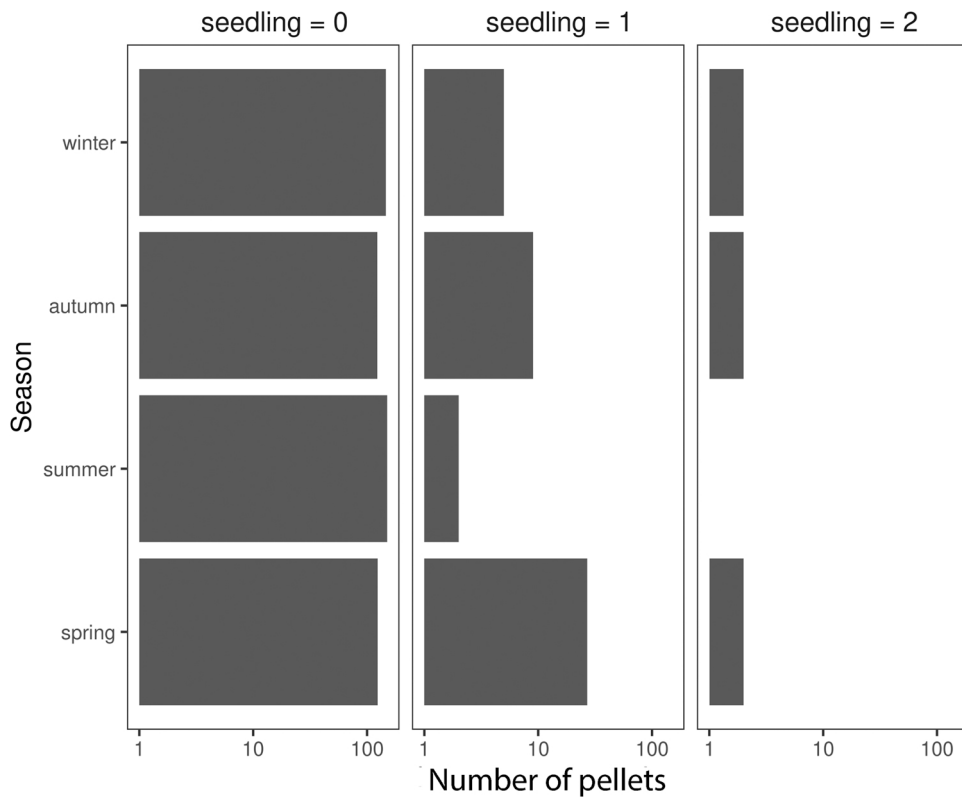


Fig. 2. Seasonal distribution and number of seedlings. The pellet with 30 germinated seedlings was excluded from the figure. The number of seedlings in the pellets was indicated above the columns.

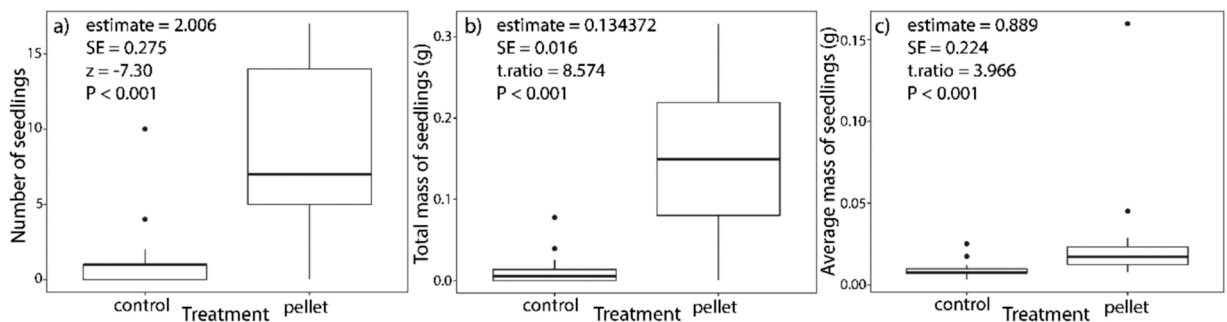


Fig. 3. Effect of pellets on the a) number of surviving seedlings, and on the b) total mass, and c) average mass of individual mustard seedlings (zero-inflated Conway-Maxwell Poisson GLM and log-linked Gamma GLM). In each pot twenty-five seeds were placed. Seedling mass was calculated from dry aboveground biomass of seedlings.

Owls preyed on common vole over other species, as it falls within the owl's preferred prey's size range and generally the most abundant and easily accessible small rodent species in the study area (Ács, 1985). In addition, in 2019, a very strong common vole outbreak has been reported from Hungary that peaked in summer (Jacob et al., 2020). This may explain the high proportions of voles in the owls' diet. Food consumption in voles reflects spatiotemporal dynamics of food availability. Although the voles are mostly herbivores (folivores), seeds are recognized as supplementary food in their diet (Fischer and Türke, 2016; Markova et al., 2020). Remains of several species' seeds (e.g., Poaceae spp., *Fragaria viridis*) was found in the stomach content of common voles by Markova et al. (2020). We also found these species in our samples. Foraging in the shallow soil layers is also known for voles which may result in unintended consumption of small seeds located there (Markova et al., 2020; Tóth et al., 2022). The generally small thousand-seed weight of the germinated species' seeds allows the opportunity for the unintended consumption during searching for roots in the soil (Markova et al., 2020). Seeds consumed by voles usually become highly damaged, or even the intact seeds found in the faeces barely germinate, so voles generally should not be regarded as seed dispersers of herbaceous plants (Markova et al., 2020; Godó et al.,

2022). However, given the high number of consumed seeds, by chance some seeds may still survive consumption. Also, by catching a foraging vole, owls may have saved seeds from chewing and some seeds might have stayed unharmed in the mouth of the victim (Grant et al., 1975; Fischer and Türke, 2016; Markova et al., 2020). Both cases may give a chance for the seeds to survive thus they could germinate from our samples.

Other prey items, including murid rodents made up a significantly smaller proportion of the owl's diet and functioned rather as a supplementary component. Unlike voles, murid rodents frequently feed on seeds and known as effective seed dispersers by scatterhoarding and endozoochory, so several tens of seeds in one pellet might be not an occasional outlier. Murid rodents usually prefer smaller seeds to consume on the spot but also feeding on relatively large seeds which they prefer to move and cache (Godó et al., 2022). The occurrence of large-seeded species in association with murid prey items imply that the seeds were consumed intentionally by the rodents (Appendix 1). Epizoochory was recorded in field mice (*Apodemus* sp.) (Kiviniemi and Telenius, 1998) and it cannot be excluded that some seeds got into our samples by this process. We can assume that not only the dominant prey item (common vole) but also other subordinate prey items can play an important role in secondary seed dispersal, despite the fact that they were present in small amounts in the diet of the owl in our study area. It is possible as the proportion of species that intentionally eat seeds increases in the owl's diet, in parallel, the role in SSD also increases. However, our dataset is not suitable for the detailed analysis of the effects of prey feeding guilds on the outcome of SSD. For establishing these associations, studies on barn owl in multiple years (i.e., in years with and without common vole outbreaks) or involving other model raptor species with even more heterogeneous diet would be needed in the future.

While shrews made up a significant proportion of the owl's diet, these species most likely do not take part in primary seed dispersal by endozoochory as they feed mostly on invertebrates (Aulagnier et al., 2018). Although seed dispersal by some of their prey species is known (e.g., by ants and slugs, Türke et al., 2010), we did not find evidence in the literature that shrews disperse seeds secondarily. Small mammals may disperse seeds by epizoochory (Kiviniemi and Telenius, 1998) but we did not find evidence for this in shrews either. These can explain why nothing germinated from the pellets that contained only shrews as prey.

The seasonal variation of the viable seed content of the pellets may be in connection with the seasonal variation in the diet of the prey species or with the seasonal changes of habitat use of the owl; however, we did not find a clear explanation for the observed patterns. We assume that a more detailed experiment may be needed to shed more light on the seasonality of SSD in the studied system. Barn owls' diet reflects the landscape composition and the farming practice of the most proper available hunting grounds. High proportion of voles and low proportion of murids is the characteristics of agro-ecosystems in the study area (Horváth et al., 2018). That is, owls probably rather used transformed areas than grasslands as hunting grounds. This can be explained by that many grasslands in the area are characterised by very short vegetation due to high intensity of grazing (Méró et al., 2015). Compared to transformed habitats with relatively higher and denser vegetation, overgrazed grassland habitats are not preferred by most rodent species because of the low availability of food and safe sites (Méró et al., 2015). Transformed habitats are characterized by disturbance-tolerant and generalist plant species, which can explain the sort of the plant species germinated from our samples.

According to the germinated plants' dispersal strategy, autochory was the most important way of dispersal. Species dispersed by rodents and owls were mostly lacking a clear morphological indication of zoochory (Sádlo et al., 2018). The fact that these species are not considered to be spread by zoochory may be because the studies that aim to categorise dispersal strategies mainly focus on large mammals and birds (Pérez-Méndez and Rodríguez, 2018). Dominance of autochory implies that these species are usually dispersed maximum a few meters away from the mother plant (Sádlo et al., 2018). This distance barely increased by dispersal only by rodents because they have a relatively small home range and disperse seeds in short- or medium distance (Godó et al., 2022). Our results showed that SSD by raptors can increase the potential dispersal distances by orders of magnitude compared to seed dispersal by rodents (see also Pérez-Méndez and Rodríguez, 2018). This service by owls supports the movement of seeds between the populations and provide access to new habitats, so ensure regional persistence of the populations, reduce the risk of local extinctions, and enhance colonization across transformed landscapes where dispersal may be otherwise restricted. Massa et al. (2015) estimated the home range of barn owls in Argentina using GPS tracking and found that it can exceed 1700 ha. This implies that the owls have the potential to disperse seeds within a large area. Furthermore, if we consider that a barn owl produces two pellets a day (Ács, 1985) and 7 % of the pellets may contain viable seeds, at least 50 viable seeds can be dispersed during a year by one individual.

Consumption by the secondary disperser can have different effects on seed viability, depending on the type of disperser. For instance, seeds in the secondary disperser's (kestrel) pellets showed reduced viability and germination compared to untreated seeds and seeds ingested by the primary disperser (lizards) only (Nogales et al., 2007). A possible explanation is that diurnal raptors possess strong digestive fluids that may decrease seed viability and germinability. In contrast, owls have much weaker digestive fluids which may have a neutral, or even a positive effect on seed germinability (Smith et al., 2021).

Our results showed that seeds deposited in pellets may gain advantage in establishment probably because they were less exposed to dehydration, and were placed in a more stable environment. Note that this germination experiment was conducted in spring, but the temperature was hotter than the average and there was no possibility for controlling the air temperature in the greenhouse. Due to this pessimal condition, the control mustard seedlings had low survival rates, which is a limitation of the experimental setup. However, it also shows the importance of the protective effect of the pellet material in extreme temperature conditions. Seedling mass in pellet-covered pots was bigger possibly because at the micro-scale, the decomposing prey remains in pellets may have increased the level of essential nutrients in the topsoil which is an important factor for the growing plants (Fedriani et al., 2015).

Though barn owls frequently roost and regurgitate pellets in places unsuitable for seed germination, but some of these sites (e.g., barns) are regularly cleaned, thus the seeds have a chance to escape these unsuitable environments. Also, when using terrain features such as trees for regurgitating the pellets, seeds have a high chance to arrive to an environment suitable for germination (Ács, 1985) and might be further dispersed by wind occasionally (Montalvo et al., 2012).

Extensive and rapid changes in land-use and climate further increase the importance of alternative dispersal agents which can

support the resilience of plant populations in fragmented landscapes. Although only a few seeds are transported by a single pellet, due to the high number of pellets produced by an individual and the facilitative effect of pellet material on seedlings owls may play an important role in long distance seed dispersal in open landscapes. Also, *Tyto* species occur worldwide so these results can be applied to other regions where similar conditions exist.

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

Data will be made available on request.

Acknowledgments

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Appendix 1. Germinated plant species with the number of pellets from which the species germinated and the micromammal taxa in the pellet. Values in the same row belong together

Plant species	No. pellets from which germinated	Prey species in the pellet (s)
<i>Alopecurus geniculatus</i>	2	<i>Microtus arvalis</i> , <i>Sorex araneus</i> <i>Microtus arvalis</i>
Apiaceae	1	<i>Apodemus</i> sp., <i>Microtus arvalis</i>
<i>Bolboschoenus maritimus</i>	1	<i>Microtus arvalis</i>
<i>Carex</i> sp.	1	<i>Apodemus</i> sp.
<i>Chenopodium album</i>	9	<i>Crocidura leucodon</i> , <i>Microtus arvalis</i> <i>Crocidura leucodon</i> , <i>Crocidura suaveolens</i> , <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i>
<i>Conyza canadensis</i>	1	<i>Crocidura suaveolens</i> , <i>Microtus arvalis</i> , <i>Sorex araneus</i>
<i>Convolvulus arvensis</i>	3	<i>Apodemus</i> sp. <i>Microtus arvalis</i> , <i>Sorex araneus</i> , <i>Sorex minutus</i> <i>Mus</i> sp., <i>Sorex araneus</i> , <i>Sorex minutus</i>
<i>Dactylis glomerata</i>	9	<i>Apodemus</i> sp., <i>Microtus arvalis</i> <i>Apodemus</i> sp., <i>Microtus arvalis</i> , <i>Mus</i> sp., <i>Sorex araneus</i> <i>Crocidura leucodon</i> , <i>Microtus arvalis</i> , <i>Sorex araneus</i> <i>Crocidura suaveolens</i> , <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> , <i>Sorex araneus</i>
<i>Digitaria sanguinalis</i>	4	<i>Arvicola amphibius</i> <i>Arvicola amphibius</i> <i>Crocidura leucodon</i> , <i>Microtus arvalis</i> <i>Microtus arvalis</i> , <i>Mus</i> sp.
<i>Epilobium tetragonum</i>	1	<i>Apodemus</i> sp., <i>Microtus arvalis</i> , <i>Mus</i> sp.
<i>Fragaria viridis</i>	1	<i>Microtus arvalis</i>
<i>Hibiscus trionum</i>	1	<i>Apodemus</i> sp., <i>Microtus arvalis</i>
<i>Lotus corniculatus</i>	1	<i>Apodemus</i> sp.
<i>Medicago lupulina</i>	3	<i>Apodemus</i> sp., <i>Crocidura suaveolens</i> , <i>Microtus arvalis</i> <i>Microtus arvalis</i> , <i>Sorex araneus</i> , <i>Sorex minutus</i> <i>Mus</i> sp.
<i>Myosurus minimus</i>	1	<i>Microtus arvalis</i>
<i>Polygonum aviculare</i>	2	<i>Microtus arvalis</i>

(continued on next page)

(continued)

Plant species	No. pellets from which germinated	Prey species in the pellet (s)
<i>Setaria verticillata</i>	5	<i>Crocidura suaveolens</i> , <i>Micromys minutus</i> , <i>Microtus arvalis</i> , <i>Sorex minutus</i> <i>Crocidura suaveolens</i> , <i>Microtus arvalis</i> <i>Microtus arvalis</i> , <i>Sorex araneus</i> , <i>Sorex minutus</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i> <i>Microtus arvalis</i>
<i>Tamarix tetrandra</i>	1	<i>Arvicola amphibius</i>
<i>Trifolium striatum</i>	1	<i>Apodemus</i> sp.
<i>Urtica dioica</i>	1	<i>Microtus arvalis</i>
<i>Vicia angustifolia</i>	1	<i>Apodemus</i> sp.
<i>Vicia hirsuta</i>	1	<i>Apodemus</i> sp.

Appendix 2. Estimated marginal means (EMM) calculated for seedling numbers across the four seasons (Conway-Maxwell Poisson generalized linear regression model)

EMMs season	emmean	SE	df	lower.CL	upper.CL
autumn	-2.4773020	0.2955961	576	-3.057879	-1.8967244
spring	-0.9501922	0.1203949	576	-1.186659	-0.7137257
summer	-5.0106357	0.9984142	576	-6.971612	-3.0496594
winter	-2.4456863	0.2717378	576	-2.979404	-1.9119685

Appendix 3. Contrasts and estimates calculated for the number of seedlings across the four season. Significant effects are marked with boldface

Contrast	estimate	SE	df	t.ratio	p.value
autumn - spring	-1.5271097	0.3191739	576	-4.784570	0.0000022
autumn - summer	2.5333337	1.0412531	576	2.432967	0.0152790
autumn - winter	-0.0316157	0.4015202	576	-0.078740	0.9372668
spring - summer	4.0604435	1.0056470	576	4.037643	0.0000613
spring - winter	1.4954941	0.2972143	576	5.031703	0.0000007
summer - winter	-2.5649494	1.0347330	576	-2.478852	0.0134658

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