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Endozoochory by the Persian fallow deer (*Dama mesopotamica*) reintroduced in Israel: species richness and germination success

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Reintroduction of herbivores may play a vital role in restoring ecosystem functions. Here we describe the role of the Persian fallow deer (*Dama mesopotamica*), reintroduced into Israel, as a vector of seed dispersal by endozoochory. Persian fallow deer have a wide diet both from grazing and browsing. From fecal samples, we found that more than 30 species of plants germinated from the deer pellets. Four of the more common species are considered as ruderal. Of the trees, carob (*Ceratonia siliqua*) seeds were the only intact seeds found in the fecal samples. We found that ingestion by the deer has a positive effect on expediting the germination of carob seeds – a factor of ecological importance in the reintroduction environment, as it contributes to plant genetic diversity by long-range seed dispersal and to community diversity.

Keywords: Persian fallow deer; *Dama mesopotamica*; endozoochory; restoration; long-range dispersal; *Ceratonia siliqua*

Introduction

Reintroductions are commonly motivated and justified by the need to enhance the survival of the species being reintroduced. However, by definition, reintroduced species are species that were at one time an integral part of the ecosystems into which they are being released, and may have fulfilled important ecosystem functions that were impeded once the local population was extirpated. Thus, reintroductions can be viewed as part of ecosystem restoration, providing further justification for the process (Polak & Saltz 2011). The species' characteristics define the general role it plays in the community and the functioning of the ecosystem. However, the extent of this role requires on-site experimentation. While it is safe to assume that large ruminants may be vectors of seed dispersal by endozoochory, the species of plants successfully transported depends on many factors, including the plant's availability, preferences of the herbivore, and the seed's ability to survive the digestion process. In some cases, the germination of hard-coated tree seeds may actually be enhanced by the passage through the digestion system of an herbivore (Rohnar & Ward 1999; Bodmer & Ward 2006; Polak et al. 2014).

Seed dispersal is a key process in determining the structure and changes in plant populations and communities and is a key factor in restoration (Poschlod et al. 2005; Poschlod et al. 2013). The dispersal of seeds is achieved via animals, wind, water, or less frequently via mechanical means of the mother plant (Cain et al. 2000; Nathan & Muller-Landau 2000). Most seeds are dispersed to a distance of only several meters from the mother plant (Schupp 1993; Caughlin et al. 2014). Therefore, rare occurrences that cause the seed to travel greater distances are important as they form new populations, drive biological invasions, change the genetic spatial structure, and affect the diversity of species and ecological communities (Cain et al. 2000; Bohrer et al. 2005; Poschlod et al. 2005; Poschlod et al. 2013). Such long-distance dispersal of seeds enhances the fitness of plants by reducing kin-competition (Hamilton & May 1977; Motro 1982a, 1982b, 1983), reducing probability of being eaten and contracting diseases or parasites, reducing inbreeding, and settling in empty spaces that are created due to environmental changes (natural or anthropogenic) (Wilson & Traveset 2000). Thus, the reintroduction of herbivores may play a vital role in restoring ecosystem functions related to long-distance seed dispersal, especially in view of other threats to biodiversity, such as fragmentation and global change (Barbet-Massin & Jetz 2014; Mokany et al. 2014). On the other hand, the restoration of functions such as seed dispersal by endozoochory may also have negative impacts, as it may enhance the dispersal of invading alien species (Myers et al. 2004; Constible et al. 2005).

In this paper, we describe the role of the Persian fallow deer (*Dama mesopotamica*) reintroduced in Israel as a vector of seed dispersal. The Persian fallow deer, previously abundant throughout western Asia, is currently endangered. In 1950, the Persian fallow deer was considered extinct. However, in 1956, a remnant population of about 24 individuals was discovered in Iran, from which a captive breeding-core was established in Europe (Chapman & Chapman 1997). In 1976, the Israel Nature Reserves Authority (currently Israel Nature and Parks Authority)

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established a breeding core of Persian fallow deer from seven (2M, 5F) deer imported from Iran and Germany for future reintroduction (Saltz 1996). Persian fallow deer are considered to be mixed feeders (Hoffman & Stewart 1972; Westoby 1978), including both grazing and browsing. Grazing constitutes over 60% of their diet and occurs year round, but in the summer and autumn the deer are forced to feed on other sources such as fruits and tree leaves (Dolev 1999). The primary goals of this study were to: (a) identify plant seeds ingested by the deer that remain vital after passing the deer gut and may, therefore, be successfully dispersed by the fallow deer, (b) determine for the seeds of tree species dispersed by the deer whether the passage through the deer's digestive system actually enhances their germination. Another vertebrate species common in the study area and large enough to consume the carob fruits is the golden jackal (*Canis aureus*). Thus, we also collected golden jackal feces and germinated the seeds within them for the sake of comparison with the fallow deer.

Methods

Identification of viable seed dispersed

As part of a long-term reintroduction program (Saltz 1998), the Persian fallow deer were reintroduced into the Soreq Valley Nature Reserve (coordinates: 31°45′N 35°04′E) in the Judean Mountains, Israel (Zidon et al. 2009). The terrain is rugged, with altitudes ranging from 450 to 800 m above sea level. Vegetation is heterogeneous, including open grasslands, garrigue with low bushes, riparian vegetation, and dense Mediterranean scrub, dominated by kermes oak (*Quercus calliprinos*) and terebinth (*Pistacia palaestina*) trees, with scattered carob (*Ceratonia siliqua*), olive (*Olea europaea*), Greek strawberry trees (*Arbutus andrachne*), and Aleppo pines (*Pinus halepensis*). The number of vascular plant species in the area is estimated as 585 species (BioGis Israel, www.biogis.huji.ac.il/Map.aspx#Vascular plants). Climate is mild, with cold wet winters and dry summers. The average rainfall between October and April is 545 mm while the average rainfall between May to September is 3.5 mm (Israel meteorological service, www.ims.gov.il). Consequently, almost no vascular plant species (except geophytes) germinate in the spring and summer (Kigel et al. 2011).

To determine which seeds are dispersed by the fallow deer via endozoochory, we collected 168 fecal samples of fallow deer for one year. The samples were collected on 10 different occasions with an average interval of 3.5 weeks between collecting occasions. All samples were collected randomly from the area within the Soreq Valley that the reintroduced population occupied (as determined by radio-tracking). Each sample, which included a large number of pellets from a single dropping, was divided into three aliquots: one-third of each sample was sown in pots in a greenhouse, one-third was sown in pots placed in the field and one-third was hand-sieved to extract the larger seeds and assess the number and the species they belonged to. The pellets were kept outside under natural conditions.

Greenhouse germination: This experiment was set up to identify the species of plants that are potentially dispersed by the fallow deer. The pellets from each sample were sown in separate 30 × 20 × 15 cm pots, each filled with commercial sterilized soil (baked at 200°F for 1 h). To control for germination from sources other than the pellet samples, 20 additional pots were prepared with the same soil but were not sown with deer pellets. The sprouts were picked the moment they could be identified, so as to minimize competition and to enhance the successful germination of seeds of other species. Due to the very large number of seeds in each pellet sample, it was impossible to transplant the seeds in separate pots.

Field germination: This experiment was carried out to assess germination success under natural conditions. The pellets from each sample were sown just before the rainy season in separate 30 × 20 × 15 cm pots placed in October 2005, in the Soreq Valley in the same area where the samples were collected. The pots were filled with local soil and may have included local seeds in addition to those in the collected pellet samples. To control for germination from sources other than the pellet samples, 42 additional pots with local soil were prepared but were not sown with deer pellets. The pots were neither watered nor protected. Sprouts were picked and identified at the end of May 2006.

Tree seed counts: The third aliquot of each sample was taken into the lab in order to identify and count the larger (tree) seeds found in the pellets. Each sample was hand-sieved and the seeds were separated from the other components in the pellets with tweezers. After the tree seeds were separated, they were identified and counted.

The effect of deer digestion on the germination of tree seeds

Because carob was the only tree species that germinated from collected deer droppings, we studied the impact of passage through the deer's digestive system on the germination of this tree species only. Carob seeds possess a hard seed coat and exhibit physical dormancy. Only a small percentage will germinate unless the coat is scarified (Piotto & Piccini 1996; Baskin & Baskin 2014). In the Soreq Valley, we found many carob seeds in the deer pellets. Another vertebrate species common in the study area and large enough to consume the carob fruits is the golden jackal *palaestina*. Thus, we also collected golden jackal feces and germinated the seeds within them.

We sowed seeds in pots on a sterile soil bed using the following treatments: (1) 228 carob seeds separated from fallow deer pellets (different pellets from those used in the section "Identification of viable seed dispersed" experiment); (2) 250 carob seeds not separated from their pods (the pods were collected from under trees); (3) 230 carob seeds that we manually exposed from pods that were collected from under trees; (4) 230 carob seeds found exposed under carob trees (i.e. the pods have disintegrated), indicating they were on the ground for a long time; (5) 70 seeds collected and separated from golden jackal feces after passing through the jackals' digestive systems; and (6) 24 seeds sown together with the fallow deer pellets within which they were found (in this treatment, we knew the number of seeds only after the end of the experiment). Sample sizes varied between treatments because we could not estimate the number of seeds in the carob pods, pellets, and feces (treatments 2, 5, and 6) and it was very difficult to locate golden jackal feces containing carob seeds. We sowed the seeds in forty 30 × 20 × 15 cm pots each divided into five sections. In each section, we sowed five seeds from the same treatment. Because we had many more seeds for some of the treatments, some pots had two sections with seeds from the same treatment.

After germination, we tagged each seedling. Two dependent variables were checked in the experiment: percentage of seeds germinating from each group and time elapsed from sowing to germination (up to 200 days). We did not assess the impact on survival because all sprouts survived the 200-day time frame of the experiment. To study the influence of passage through the deer digestive system on germination, we compared the results of treatment (1) to each of the treatments (2), (3), and (4). To compare the two different digestive systems (deer vs. jackal), we compared the results of treatment (1) with treatment (5). To study the influence of the pellets on germination rate, we compared treatments (1) and (6). Differences in the proportions of germination were tested using two-tailed Fisher's exact test, with a Bonferroni adjustment of α (five comparisons were planned). Thus, we considered results to be significant at a P value smaller than 0.01. There are several theories regarding the presentation of a two-sided probability in a Fisher's exact test (Agresti 1992). Here we employed the strictest approach of doubling the single-sided probability.

Results

Identification of viable seed dispersed

Greenhouse germination: More than 30 plant species germinated from the deer pellets in the greenhouse pots (Table 1). There was no germination in the control pots. Eleven species constituted more than 93% of the sprouts. The most common species was *Chenopodium album* (almost 47%). A total of 20 carob sprouts germinated in 7.7% of the samples.

Field germination: Eight species germinated in the pots (both in control pots and pots with deer pellets), including: *Filago pyramidata, Anagallis arvensis, Conyza canadensis, Chenopodium album, Cistus incanus*, one species of cereal and two species from the genus *Trifolium* that could not be fully identified. All species that germinated in the field pots germinated in the greenhouse as well. Six of the eight species had more sprouts in pots containing deer pellets than in pots with local soil only, and the difference was significant for three of these species: *Filago pyramidata*, *Chenopodium album*, and one of the *Trifolium* species ($t_{94} = 2.459$ $P = 0.016$, $t_{81} = 2.767$ $P = 0.007$, and $t_{81} = 2.990$ $P = 0.004$, respectively − all by two-tailed t-tests assuming unequal variances). The mean number of sprouts in pots with deer pellets was significantly higher than pots not containing deer pellets ($t_{107} = 3.236$ $P = 0.0001$, one-tailed t-test assuming unequal variances).

Tree seeds: One hundred fifty four seeds were found in 60% of the fecal samples that were hand-sieved. All of these seeds were carob (*Ceratonia siliqua*) seeds.

Table 1. The number of seedling and number of pellet group occurrences for germinated seeds.

Species	Number of seedlings	Percentage of pellets	Species	Number of seedlings	Percentage of pellets
Chenopodium album	661	29%	*Bromus madritensis*	4	1%
Solanum nigrum	171	18%	*Bromus sterilis*	4	1%
Conyza canadensis	129	21%	*Cistus incanus*	3	<1%
Polygonum lapathifolium	111	16%	*Sonchus oleraceus*	3	<1%
Filago pyramidata	65	10%	*Malva sylvestris*	2	<1%
Polygonum equisetiformis	50	16%	*Sorghum halepense*	2	<1%
Chenopodium murale	37	6%	*Apium nodiflorum*	1	<1%
Piptatherum miliaceum	29	10%	*Cuscuta campestris*	1	<1%
Trifolium tomentosum	27	9%	*Daucus carota*	1	<1%
Anagallis arvensis	23	8%	*Geranium purpureum*	1	<1%
Ceratonia siliqua	20	8%	*Legousia falcata*	1	<1%
Solanum lycopersicum	17	5%	*Melilotus sulcatus*	1	<1%
Trifolium campestre	17	6%	*Parietaria judaica*	1	<1%
Trifolium sp.	13	4%	*Paspalum paspalodes*	1	<1%
Dittrichia viscose	6	2%	*Parietaria judaica*	1	<1%
Medicago polymorpha	5	1%	*Trifolium purpureum*	1	<1%
Amaranthus viridis	4	<1%	*Trifolium* sp.	1	<1%
Brachypodium distachyon	4	<1%	Poaceae sp.	1	<1%

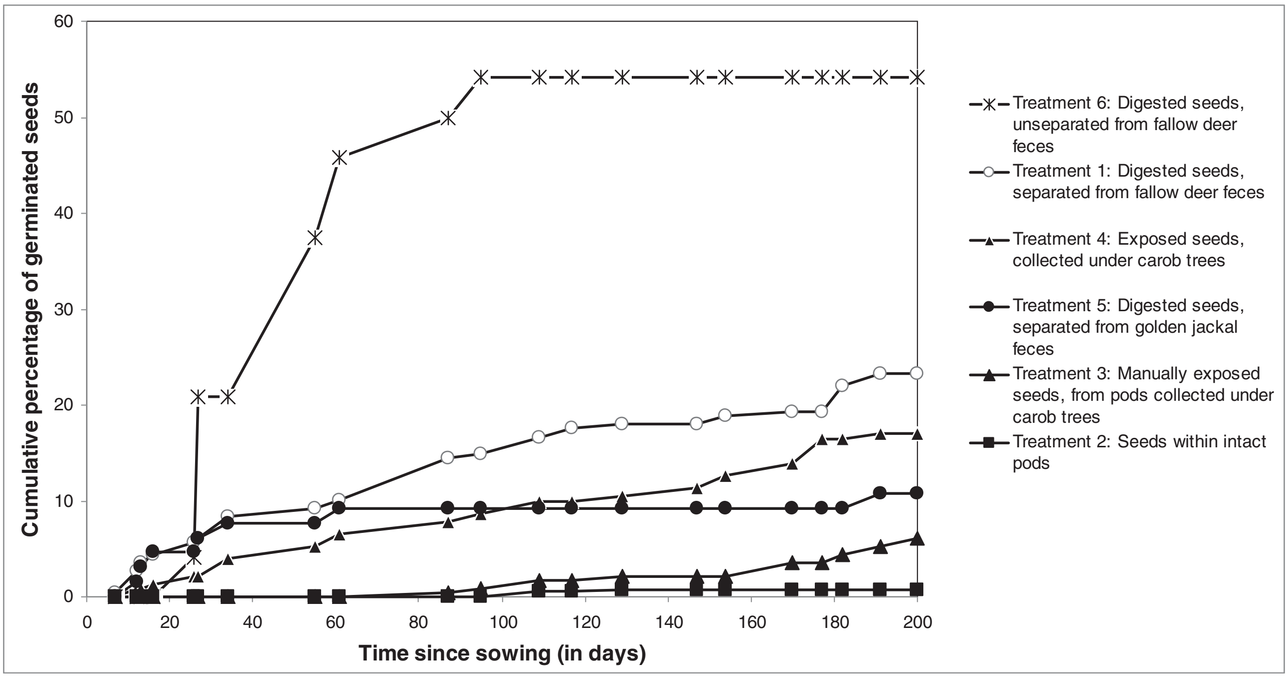

Figure 1. Cumulative percentage of germinated carob seeds during the time since sowing day, for the various treatments.

The effect of deer digestion on carob germination

Germination rate, calculated as the proportion of seeds germinating within 200 days from sowing, was significantly higher for digested carob seeds (separated from the deer pellets, treatment 1) than for seeds within their pods (treatment 2; 23.25% vs. 1.20%, two-tailed Fisher's exact test, $P < 0.001$) and seeds that were manually exposed (treatment 3; 23.25% vs. 5.22%, two-tailed Fisher's exact test, $P < 0.001$). Digested carob seeds did not germinate significantly faster than carob seeds collected under trees (23.25% vs. 16.96%, two-tailed Fisher's exact test, $P = 0.118$). Digested carob seeds, separated from Persian fallow deer pellets, germinated faster (albeit not significantly after applying the Bonferroni adjustment) than carob seeds separated from golden jackal feces (treatment 5; 23.25% vs. 10.00%, two-tailed Fisher's exact test, $P = 0.019$). However, digested carob seeds separated from Persian fallow deer pellets germinated slower than digested seeds that were not separated, but sown with the deer feces (treatment 6; 23.25% vs. 54.17%, two tailed Fisher's exact test, $P = 0.004$ – Figure 1). No significant difference was found in the survival of sprouts from any of the groups.

Discussion

The dispersal of seeds by cervids is well known and has been previously documented (Mouissie et al. 2005; Yamashiro and Yamashiro 2006; Williams et al. 2008). Similar to the first part of our study, these studies focus on the species of seeds that are viably transported. However, endozoochory by ungulates may play a major role in the germination dynamics of large hard-coated seeds, as the ingestion of such seeds by these animals may enhance their germination (Rohner & Ward 1999; Bodmer & Ward 2006; Polak et al. 2014). Here, we followed our identification experiment with experiments on germination dynamics focusing on large, hard-coated tree seeds we identified in the first experiment – in this case, with carob seeds only. These experiments assessed the effect of the digestive process on germination dynamics by sprouting seeds from different sources and under different conditions. We considered this important because the carob is an important species in the semi-arid Mediterranean that provides, amongst other things, nutritious pods and green forage to herbivores during the dry season.

Various studies have linked seed germination rate with ruminant body mass. Thus, Peled (2010) showed that germination rate of acacia seeds is higher for the Arabian oryx than for the smaller dorcas gazelle, and Stavi et al. (2015) reported decreasing germination rates of acacia seeds with smaller body size of three ruminant species – addax, Arabian oryx, and dorcas gazelle. In contrast, Tjelele et al. (2015) reported a larger germination rate for domestic goats than for cattle, but they demonstrated the enhancing effect of the dung as a fertilizer on seedling establishment.

While other vertebrate species such as bats (Izhaki et al. 1995) and jackals (this study) disperse carob seeds in our study ecosystem, our findings suggest that the Persian fallow deer do not only contribute to the carob population by ingesting and dispersing their seeds, but that the relatively large body size and the deposition of the seed with the organic matter of the pellets substantially increase germination rate.

Thus, the deer have a strong positive effect on the dynamics of carob which is also an important food resource for them, indicating a potentially co-evolutionary process. This, in turn, indicates a possible cascading effect following the extirpation of ungulates. This may cause a significant shift in plant community structure and dynamics

Table 2. Proportion of carob seeds germinating within 200 days, and the conditional average time to germination (of seeds that germinated within 200 days) in the six different treatments.

Treatment	Number of seeds	Proportion of seeds germinated within 200 days	Conditional average time (days ± SD) to germination*
1. Digested carob seeds, separated from fallow deer pellets	228	23.25%	85.64 ± 62.53
2. Seeds within intact pods	250	1.20%	115.67 ± 23.09
3. Manually exposed seeds, from pods collected under carob trees	230	5.22%	156.07 ± 42.27
4. Exposed seeds, collected under carob trees	230	16.96%	102.62 ± 60.82
5. Digested seeds, separated from golden jackal feces	70	10.00%	50.57 ± 64.23
6. Digested seeds, unseparated from fallow deer pellets	24	54.17%	22.53 ± 15.01

*Of seeds that germinated within 200 days.

and ultimately other extinctions, further highlighting the importance of the reintroduction of ungulates.

In addition to the carob seeds, the reintroduced Persian fallow deer distributed viable seeds of more than 30 other species. Most of these species do not possess features typical of species that are dispersed by animals, and fit Janzen's (1984) theory of "the foliage is the fruit." Twenty of these species are annuals while the others are perennial plants. With the exception of *Cuscuta campestris*, none of the dispersed species has any kind of thorns (that would facilitate their dispersal by exozoochory). Three of the dispersed species, *Polygonum lapathifolium, Cuscuta campestris*, and *Apium nodiflorum,* are rare in the study area, and one, *Cuscuta campestris*, is considered invasive. The home range of Persian fallow deer in our study region varies in size from 86 to 365 ha (Dolev et al. 2002; Perelberg et al. 2003; Bar-David et al. 2005). Coupled with the expected long gut retention time (up to 96 hours in the European fallow deer – Mouissie et al. 2005), and the fact that deer pellets were found in all types of habitats of the reintroduction site, we conclude that the deer are important vectors for long-range seed dispersal, potentially dispersing seeds to 1 km and occasionally beyond that.

While many of the seeds ingested by ruminants may be destroyed by either teeth grinding or the digestive system (see e.g. Rohner & Ward 1999; Fragoso et al. 2003), others may survive the process and even benefit from it. The improvement of the sprouting ability of an ingested seed can manifest itself not only in a higher probability and speed of sprouting, but also in increased growth rate of the seedling (Howe 1986; Polak et al. 2014). In the greenhouse experiment, 18 plant species had less than five sprouts per species. The low number of sprouts may indicate that the digestive system of Persian fallow deer has a negative effect on the seeds of these plant species. Similar results were documented for the European fallow deer (Mouissie et al. 2005). However, because most seeds end up at a distance of only several meters from the mother plant (Howe & Smallwood 1982), rare occurrences that cause the seed (even a singleton) to travel greater distances become important if most seeds are destroyed in the digestive process. In addition, the low number of sprouts may be indicative of low seed production of the species (Bruun & Poschlod 2006) or of foraging preferences. Thus, while endozoochorous seed dispersal by deer may seem of little importance to the dynamics of the plant community (Veen 2003; Mouissie et al. 2005), the common occurrence of viable seeds of many species that may be transported over large distances (Cain et al. 2000; Caughlin et al. 2014) in combination with enhanced germination makes endozoochory a key function in shaping vegetation structure even if a significant proportion of ingested seeds is destroyed in the process. Specifically, the surviving seeds can form new populations, drive biological invasions, drive changes in the genetic spatial structure and changes in the structure of ecological communities (Hanski & Gilpin 1997; Harper 1977; Cain et al. 2000).

As for the carob, expediting its germination may help the sprouts, because carob fruits (in this area) are fully developed by July–August (dry season). A seed that germinates at the beginning of the mild winter may have a better chance to survive, compared to a seed that germinates at the end of the winter or in the hot and dry spring. In addition, shortening the dormancy period of a seed can presumably decrease its probability of being eaten by seed predators.

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