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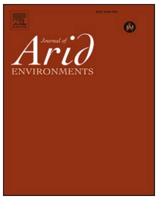

Seed dispersal by carnivores in a hyper-arid habitat: insights from the Sahara Desert

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ABSTRACT

We investigated the role of carnivore mammals as seed dispersers in a Saharan environment, where alternative dispersers are scarce. First, we studied the frequency of occurrence (FO) of seeds in scats and assessed fruit selection by comparing use versus availability. Second, we evaluated seed dispersal by measuring the density of undamaged seeds disseminated and examining the presumed differences between optimal and sub-optimal macro-habitats for germination. Seeds from eight plant species (*Ziziphus lotus*, *Lycium shawii*, *Asparagus altissimus*, *Searsia tripartita*, *Nitraria retusa*, *Phoenix dactylifera*, *Ephedra alata*, and *Balanites aegyptiaca*) were found in 597 collected fecal samples from four carnivore species (North African golden wolf *Canis lupaster*, red fox *Vulpes vulpes*, Rüppell's fox *V. ruepellii*, and honey badger *Mellivora capensis*). The FO ranged 9.47% to 35.29% per species and study period. Wolves preferentially consumed the drupes of *Z. lotus,* while foxes selected the berries of *L. shawii* and *A. altissimus.* On average, 12.9 ± 2.4 intact seeds/scat were found in the samples containing seeds, with 72.4% of these seeds deposited in optimal habitats (dry riverbeds and secondary ravines), amounting to 1038.9 ± 351.1 undamaged seeds/km^2. Our results suggest an important role of canid species as seed dispersers in the Sahara Desert.

1. Introduction

Seed dispersal by animals is a key ecological process that involves the consumption of fruits and the subsequent passage of seeds through the digestive tract, after which they are excreted away from the parent plant (Dennis, 2007; Fleming and Estrada, 2012). This process is generally advantageous for plant fitness, although it also depends on additional factors that influence seed survival and germination (McConkey and Drake, 2006; Schupp et al., 2010; Viana et al., 2013). The role of animals is therefore vital for plant distribution, demography, and even the composition of plant communities (Triay-Limonta et al., 2024). Mammalian carnivores can play a pivotal role as seed dispersers of fleshy-fruited plants (Rubalcaba-Castillo et al., 2020; Herrera, 1989; Escribano-Avila, 2019). They are capable of consuming a wide variety of fruit sizes and types (Fedriani and Delibes, 2009; López-Bao and Gonzalez-Varo, 2011; Zhou et al., 2013). They ingest large quantities of fruits and defecate the seeds with minimal mechanical damage, mainly due to limited mastication, and numerous studies show that the passage of seeds through the digestive tract often enhances seed viability and improves germination rates (Fedriani and Delibes, 2009; Cancio et al., 2016, 2017). In addition, their extensive spatial requirements make them especially important as long-distance seed dispersers, enhancing plant population connectivity and facilitating colonization (Draper et al., 2022).Carnivores can deposit seeds in different microhabitats compared to other frugivores (Escribano-Avila, 2019) which can influence the effectiveness of seed dispersal, such as the optimal location

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with the highest probability of seed germination and survival (Arnberg et al., 2024).

The frugivory capacity in carnivores is greatly influenced by the diverse physical capacities of taxa within the order. Indeed, some species consume fruits directly from trees by climbing, as observed in taxa such as Viverridae, Ursidae, and Mustelidae (Draper et al., 2022; Mudappa et al., 2010; Takatsuki et al., 2018). Conversely, other species feed on fruits only after they have fallen to the ground when ripe, a behavior presents in taxa within Canidae and Mustelidae (Herrera, 1989; Enders and Vander Wall, 2012; Grünewald et al., 2010).However,despite the fundamental role these endozoochorous animals play in some ecosystems, various biotic and abiotic factors can limit their benefits. For instance, the quality of seed dispersal is often more strongly influenced by the characteristics of deposition sites than by the mere distance seeds are moved or by their quantity (Rubalcava-Castillo et al., 2021).

The Sahara Desert is one of the most significant hyperarid regions on Earth (Draper et al., 2022). Although few studies have examined the diets of carnivore species there (Brahmi et al., 2012; Karssene et al., 2019; Gil-Sánchez et al., 2020), important ecological gaps remain regarding animal-mediated seed dispersal mechanisms, specifically by carnivores, and their role in plant communities (Draper et al., 2022). Furthermore, the limited research on endozoochorous seed dispersal by carnivores in arid environments reflects the generally lower presence of zoochorous plant species in these ecosystems (Shikesho et al., 2024). Such species tend to decrease in dry climates, in contrast to their abundance in tropical and humid forests, where this dispersal mechanism is more widespread (Fleming and M Stoddart, 1979). Therefore, we aim to expand current understanding by identifying which specific plant species are dispersed by carnivores in the Sahara Desert, and which carnivore species act as their dispersal agents. Additionally, we seek to explore: (1) the preferences of carnivores for certain fruits over others, and (2) the magnitude of seed displacement by carnivores (i.e., the number of seeds dispersed) and the likelihood of their deposition in optimal environments suitable for germination. Considering that the Sahara is one of the most poorly preserved ecoregions on Earth (Durant et al., 2014; Gil-Sánchez and Sánchez-Cerdá, 2023), studies like ours are essential to generate the knowledge needed for the effective conservation of this largely understudied ecosystem.

2. Methods

2.1. Study area

The study area is situated in the Atlantic Sahara of Morocco, between the lower Draa River and the basin of Sequiat al Hamra, forming a rough ellipse of around 20,000 km^2 between latitudes 11°30′W and 9°30′W and longitudes 28°30′**N** and 27°0′N (Fig. 1). The climate is arid and hot and corresponds to a low-latitude subtropical desert in the Köppen-Geiger classification – BWh (Beck et al., 2018). Mean temperature ranges from 22.7 °C in the west to 23.2 °C in the eastern inland areas, with annual precipitation averaging from 138 mm to 59 mm. This region represents the southernmost limit of Macaronesian-type vegetation —mostly confined to ravines and represented by the argan tree (*Argania spinosa*) —and the northernmost boundary of Saharan vegetation, where the acacias *Vachellia tortilis* and *V. ehrenbergiana* are the dominant trees. It forms part of the North Saharan Xeric Steppe and Woodland ecoregion (Olson et al., 2001).

The study region serves as an important refuge for wildlife. Moreover, due to its geographical position bordering the Atlas Mountains, it harbors a rich diversity of flora, including numerous species adapted to semi-desert and arid climates. The carnivore community comprises 12 species across 6 families (Gil-Sánchez et al., 2020; Aulagnier et al., 2017): 4 species of canids (African golden wolf *Canis lupaster*; red fox *Vulpes vulpes*; Rüppell's fox *V. rueppellii;* fennec *V. zerda*), 3 species of felids (African wildcat *Felis lybica*; sand cat *F. margarita;* caracal *Caracal caracal*), 2 mustelids (honey badger *Mellivora capensis;* Saharan striped weasel *Ictonyx libyca*), 1 viverrid (common genet *Genetta genetta*), 1 herpestid (Egyptian mongoose *Herpestes ichneumon*), and 1 hyenid (striped hyaena *Hyaena hyaena*). Among these, all canids, honey badgers, common genets, and striped hyaenas are potential seed dispersers, based on their diet (Gil-Sánchez et al., 2020; Wilson and Mittermeier, 2009).

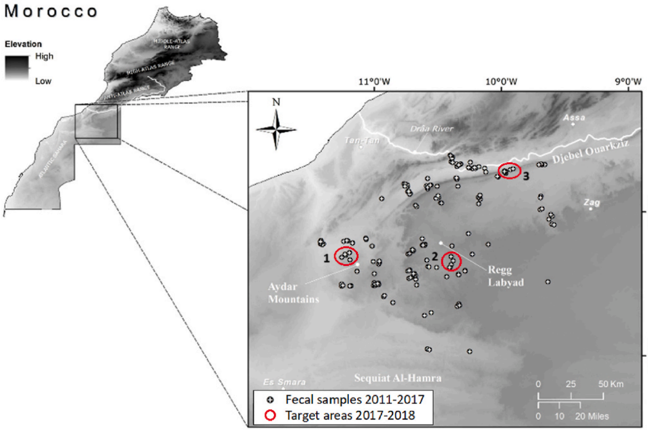

Fig. 1. Location of the study area and main topological names. The Drâa River delineates the northern boundary of the Saharan bioclimatic zone. Red circles indicate sampling areas where fruit sampling was conducted, following the same tracks used for carnivore scat collection: 1) Aydar mounts, 2) oued Taclet, 3) djebel Ouakziz. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Regarding zoochorous plant species that produce fleshy fruits in our study area and are likely to be consumed by animals in arid environments, they tend to be very scarce (J.M. Gil-Sánchez and I. Cancio, per. obs.). Nevertheless, according to (Herrera, 1989) and (Debussche and Isenmann, 1989) (i.e., carnivores preferentially consume certain fruit species of trees and shrubs whose fruits emit a scent, fall to the ground when ripe, and are generally rich in water and sugars while being low in lipids and proteins), we identified at least nine species that produce nutritious berry-like/drupaceous fruits that could potentially be dispersed by carnivorous mammals:

Ziziphus lotus, Rhamnaceae. Xerophytic shrub distributed across North Africa and the western Mediterranean, where it predominantly occurs in arid and semi-arid environments, with fragmented relict populations persisting in the south-eastern Iberian Peninsula. The species produces fleshy drupaceous fruits (9–12 mm in diameter), and previous studies have reported seed dispersal by carnivores, including *Vulpes vulpes*, in the semi-arid south-eastern Iberian Peninsula (Cancio et al., 2017).

Lycium shawii, Solanaceae, produces small red berries (globose, 3–5 mm in diameter) and is distributed across arid and desert environments throughout the Middle East, North Africa, East Africa, and western Asia. Studies on closely related *Lycium* species (e.g., *L. intricatum* and other congeners) have shown that birds and other vertebrates consume the berries and disperse the seeds. These vectors may contribute to secondary dispersal processes such as diploendozoochory, in which seeds previously ingested by one animal are subsequently dispersed by secondary predators (e.g., raptors consuming lizards containing seeds) (Nogales et al., 2002).

Asparagus altissimus, Asparagaceae, produces berry-like fruits approximately 4–10 mm in diameter and is distributed across arid and desert regions of northwestern and western Africa. Seed dispersal has been documented in other species of the same genus, with birds playing a significant role in their dissemination (Debussche, 1985).

Searsia tripartita, Anacardiaceae, produces round, fleshy drupes measuring approximately 5–6 mm in diameter (J. M. Gil-Sánchez and I. Cancio, per. obs.). To date, there are no published studies addressing its seed dispersal mechanisms.

Nitraria retusa, Zygophyllaceae. It is a drought-tolerant, halophytic shrub that grows in arid and saline environments. The species produces berries measuring 6–12 mm in diameter and is distributed across North Africa and the Middle East. Domestic animals grazing on this plant include sheep, goats, and camels, which consume its leaves and branches (Shaltout, 2003).

Phoenix dactylifera, Arecaceae, produces fruits 15–30 mm in diameter, each containing a single elongated seed measuring 2–3 cm, embedded in a sweet, sugar-rich pulp. Although native to the Middle East and western Asia, its distribution is broader due to cultivation and use as an edible fruit, reaching North Africa. Recent studies document vertebrate-mediated dispersal, including by birds, bats, and canids such as domestic dogs (Spennemann, 2018; Sayedi et al., 2022).

Ephedra alata, Ephedarceae, is a gymnosperm that produces strobilar cones with a fleshy structure surrounding the seed. The cones are ovoid to globose, measuring 3–5 mm in diameter, and its distribution is primarily Saharo-Arabian. The seeds can be dispersed by birds and small mammals (González-Varo et al., 2022).

Balanites aegyptiaca, Zygophyllaceae, produces fleshy drupaceous fruits containing a hard seed, measuring 10–25 mm in diameter, and occurs in arid and semi-arid regions of Africa and western Asia. Its fruits can be dispersed by birds and mammals (Okia, 2010).

Argania spinosa, Sapotaceae, produces fleshy drupaceous fruits containing a hard seed, 15–20 mm in diameter. It is endemic to southwestern Morocco, with small populations in western Algeria. The large seed is not readily dispersed through the digestive tract; however, a dispersal mechanism has been described involving ungulates, such as goats, which regurgitate the seed intact during rumination, representing a form of vertebrate-mediated endozoochory (El Aich et al., 2007).

To analyze the potential qualitative component of seed dispersal, we focused on two main macro-habitats (Gil-Sánchez et al., 2024): (1) oueds and secondary ravines, which concentrate most of the target plant species due to their higher soil moisture; and (2) regs and rocky areas, which generally lack these plants for the opposite reason. Oueds are ancient rivers that are usually dry but can contain ephemeral surface water during rainy years. Regs are gravelly or sandy flat areas, while rocky habitats are mainly found in mountainous and hilly areas called djebels, as well as in some parts of regs. At the landscape scale, regs and djebels are the dominant habitats (Gil-Sánchez et al., 2024).

2.2. Field surveys

Field surveys were conducted during two distinct sampling periods. In the first period, we surveyed carnivore scats across the entire study area to capture maximum spatial and temporal variability. Faecal samples were collected during 14 expeditions (two expeditions each year, one in spring (April) and another in winter (December–January), each lasting 9 days, conducted between April 2011 and April 2017. A total of 43 sampling areas (c.a. 25 km^2 per area on average) were surveyed (Fig. 1) searching for carnivore faeces. We carried out 1–3 walking surveys per study site (one person each), covering 3 to 23 km walked per survey (mean = 11.1 km, SE = 0.51 km), resulting in 86 walking surveys (954 km in total), spanning all available habitats. All carnivore faecal samples were georeferenced using a portable GPS. Field scat identification was performed by experienced personnel based on faecal size and morphology before placing samples in paper bags; all the collected scats appeared to be intact. Environmental conditions were sufficiently dry to preserve the samples without the need for desiccants, since as dryness favours long-term preservation of faecal material (Mitelberg et al., 2019). Sampling was conducted during two distinct seasonal periods to capture variability in primary productivity: December-January, representing the high productivity that occurs during periods of low photosynthetic activity or after periods of high rates of reserve accumulation (Jordano and Fenner, 1992) and March-April, a low-productivity season. The hottest months (May-September) were deliberately avoided due to severe logistical constraints and the challenging working conditions for field personnel. Both sampling periods cover the fruiting season of the targeted plant taxa (data from this study).

During the second sampling period, we collected specific data on seed dispersal by carnivores and fruit availability across two different seasons: December-January 2017 (i.e., autumn-winter) and May 2018 (i.e., spring). These sampling efforts coincided with a period of regional drought (see details in (Gil-Sánchez et al., 2024)]) and covered the local fruiting peaks. Prolonged periods of drought significantly affect the phenology of plant species in deserts, particularly their flowering and fruiting patterns. In fact, fruit production is highly dependent on optimal water conditions for their development (Flexas et al., 2021), and during such periods, the production of fleshy fruits (berries/drupes) may be affected. Therefore, it is important to establish two distinct seasonal sampling periods to capture different stages of the fruit cycle, considering the high variability both among species and across zones.

The sampling areas located in djebel Ouarkziz, oued Taclet and Aydar mounts (Fig. 1), represent the full range of regional environmental heterogeneity for the listed plant species. We did not sample reg habitats as they lack the target plant taxa; therefore, we assumed that even if seeds were deposited, they would be unlikely to germinate (Bouallala et al., 2022). We collected carnivore scats and simultaneously estimated plant abundance and fruit availability along two walking transects per sampling area in December-January 2017, and along a single walking transect per sampling area in May 2018 due to logistical limitations, using the same tracks as those from the winter survey. The transects were conducted by two observers and ranged 10.8 km to 17.7 km (124 km of accumulated effort), covering a width of 4 m for the scats survey and 8 m for the vegetation survey. Only scats with a recent appearance were collected to ensure temporal overlap with fruit surveys. For each scat, we recorded whether the habitat was potentially optimal for germination at macro-habitat level; areas with presence of the targeted plant species were considered optimal, exclusively oueds and secondary ravines, while we considered non-optimal the rest areas (without these species, usually rocky areas).

Fruit availability was sampled from up to 15 selected individuals per targeted plant species along each transect and in each season, through choosing the first detected individual each 10 min walking (c.a. 200 m intervals) when possible; this distance was selected to ensure that we could detect 15 individuals before the transect ended. Following (Herrera and García, 2009), we carried out semi-quantitative estimates based on a Fruits Abundance Index (FAI): where FAI 0 = no fruits; FAI 1 = 1–10 fruits; FAI 2 = 11–100 fruits; FAI 3 = 101–1000 fruits; FAI 4 = 1001–10,000 fruits; and FAI 5 = more than 10,000 fruits. This index was applied to the nine previously listed freshy fruits plants species.

2.3. Data analysis

The species to which the scat belonged and which were collected during the first period were identified at species level using DNA analyses based on genetic barcoding (see details in (Gil-Sánchez et al., 2024)). Due to the high agreement between field identification and DNA confirmation (>90%), scats collected during the second period were visually identified at the genus level. In this case, we were unable to distinguish between red fox and Rüppell's fox; therefore, the samples from both canids were pooled for analysis. In the laboratory, the scats were manually broken apart to search for seeds, which were identified using a reference collection collected in the study area. For each scat, we counted and classified all seeds as either undamaged or damaged.

From the average FAI interval obtained for each species and based on the principle of linear interpolation (Herrera and García, 2009), we calculated the number of fruits by mathematical interpolation using the formula: $f(x_1)+((fx_2-fx_1)/(x_2-x_1))*(FAI-f(x_1))$, where $f(x_1)$ is the smallest value of the FAI interval; $f(x_2)$ is the largest value of the FAI interval; x_2 corresponds to the next integer of the FAI average, and x_1 corresponds to the integer that is below the FAI average. The abundance of fruits per hectare and per species was then obtained by dividing the estimated number of fruits by the transect area, calculated as the transect length multiplied by an 8 m width.

The analysis of fruit selection by each carnivore species was carried out by comparing availability versus use/consumption. The proportion of availability (%) was obtained from the total abundance of fruits per hectare, while the frequency of occurrence (%, assumed as a proxy for use/consumption (Herrera, 1989; Cancio et al., 2017; Mudappa et al., 2010)) derived from the scats collected during the fruit surveys was used to quantify the selection of each plant species through Ivlev's electivity index; its p-value was calculated using 2x2 chi^2 contingency tables.

Following (Miller, 1996), we estimated the abundance of dispersed seeds within apparently optimal macro-habitat for germination, based on the transects conducted during the second sampling period. First, we divided the six transects in sub-samples of 200 m, resulting in 623 sub-samples. Second, we calculated the number of intact seeds per plant species and hectare dispersed by each carnivore species, through multiplying the average number of detected seeds per faecal sample (containing seeds) by the number of faeces containing seeds/ha. The number of faeces/km^2 was calculated using data from the 623-200 m subsamples (4 m × 200 m = 0.08 ha per sub-sample). The average ± SE abundance of dispersed seeds was compared between the two surveyed macro-habitats (oueds and secondary ravines versus other habitats) using t-tests. Finally, we calculated the ratio between the dispersed seeds/ha and the available fruits/km^2 for the optimal habitats (as no available fruits were recorded in suboptimal habitats).

Due to limitations in sample size (i.e., the number of faeces containing seeds; see Results section), we pooled all the spatial and seasonal data to estimate the fruit selection and the seed dispersal. Nonetheless, both sampling periods covered the fruiting season of the targeted plant species.

3. Results

We obtained a total of 597 fecal samples from seven carnivore species; 415 samples collected during the first period of the study, and 182 samples during the second. Some carnivores present in the study area had a very low presence in the sample, or we failed to detect their scats (Table 1). Seeds were detected in 67 samples (11.2%), corresponding to four species of carnivores: three canids (African golden wolf, red fox, Rüppell's fox) and one mustelid (honey badger). The frequency of occurrence (FO) ranged from 9.47 to 35.29%, depending on species and study period (Table 1). The consumed fruits belonged to eight species of plants (Table 2). On average, 12.9 ± 2.4 seeds/scat were found undamaged (N = 67 scats).

During the second period of the study, scats containing seeds were found only for African golden wolves and foxes; no seed-containing scats were recorded for honey badgers (Table 1). Information on plant species abundance and fruit availability is presented in Fig. 2, which summarizes data from 1571 surveyed individuals. The species with the highest fruit production were *S. tripartita* (up to 6906 fruits/ha in oued Taclet) and *A. spinosa* (up to 425 fruits/ha in the djebel Ouarkziz), followed by *L. shawii*, and *A. altissimus* (up to 87 fruits/ha and 21 fruits/ha, respectively, in the Aydar mounts), all recorded during winter. We detected different patterns of fruit selection: wolves primarily selected the drupes of *Z. lotus,* while foxes selected the fruits of *L. shawii* and *A. altissimus* (Fig. 3). Notably, most of jujube fruits (*Z. lotus*) found in fox scats were selected by red fox, as Rüppell's foxes disappeared from the djebel Ouarkziz and the Aydar mounts during the second period of the study (Gil-Sánchez et al., 2024).

On average, 609.5 ± 154.1 undamaged seeds/km^2 were dispersed by canids, with foxes being the species showing the highest values (Fig. 4). Most of the seeds (72.4%) were found within optimal habitats (oueds and ravines), resulting in significant difference (*t*-test = 2.09, P = 0.037, n = 621) between both habitats in the abundance of dispersed seeds. Specifically, 1038.9 ± 351.1 undamaged seeds/km^2 were recorded in oueds and ravines (58.0 km of sampling effort), compared to 301.5 ± 122.1 undamaged seeds/km^2 in rocky areas (66.6 km of sampling effort). All seeds dispersed by honey badgers (detected only during the first part of the study) were found in two latrines located in suboptimal sites for germination (rocky soils at the base of cliffs). The ratio between dispersed seeds and available fruits was highest for drupes *of Z. lotus* and low to very low for the other species (Fig. 4). This ratio could not be calculated for *P. dactylifera*, as no fruiting trees were detected during the surveys.

Table 1
Occurrence of seeds in 597 carnivore mammals faecal samples collected in the North Atlantic Sahara.

Species	Period	Collected scats	Scats with seeds	% Scats with seeds
African golden wolf	2011-2017	78	18	23.07
African golden wolf	2017-2018	34	12	35.29
Red fox	2011-2017	39	9	9.47
Red fox	2017-2018	95	17	17.89
Honey badger	2011-2017	107	0	0
Honey badger	2017-2018	86	10	11.62
North African wildcat	2011-2017	92	0	0
North African wildcat	2017-2018	53	0	0
Rüppell's fox	2011-2017	6	1	16.66
Rüppell's fox	2017-2018	0		
Fennec fox	2011-2017	3	0	0
Common genet	2011-2017	2	0	0
Striped hyaena	2011-2017	2	0	0
Saharan striped polecat	2011-2017	0		
Sand cat	2011-2017	0		
Caracal	2011-2017	0		
Egyptian mongoose	2011-2017	0		

Table 2
Number of seeds per plant species detected and their occurrence in faecal samples of four carnivore species collected in the North Atlantic Sahara between 2011 and 2018.

Species	African Golden wolf		Red and Rüppell's foxes		Honey badger	
	Seeds	Scats	Seeds	Scats	Seeds	Scats
Phoenix dactylifera	60	7	5	1	34	10
Ziziphus lotus	102	14	67	5	0	0
Searsia tripartita	9	3	211	4	0	0
Nitraria retusa	47	2	48	1	0	0
Lycium shawii	4	1	128	7	0	0
Ephedra alata	11	2	0	0	0	0
Asparagus altissimus	32	1	77	4	0	0
Balanites aegyptiaca	2	1	0	0	0	0
N.I.	60	3	24	6	0	0
Total	327	33	560	28	34	10
Total scats		112		134		193

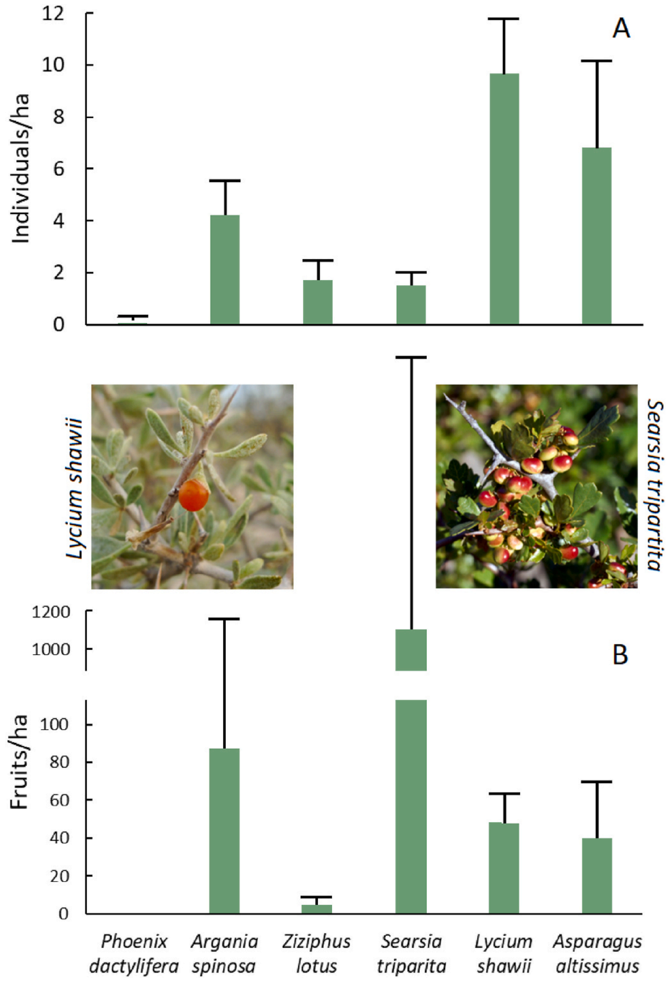

Fig. 2. Plant species (A) and fruit abundances (B) in three sampling areas of the North Atlantic Sahara Desert. Error bars show standard errors.

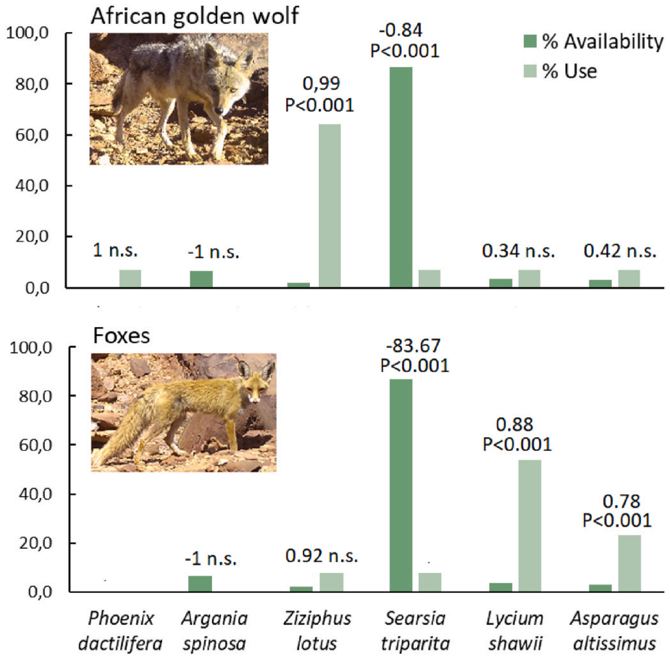

Fig. 3. Fruit selection by canids in the North Atlantic Sahara Desert. Ivlev's electivity index (ranging from −1 to 1, where negatives values indicate avoidance and positive values indicate selection) and its P-level are shown. % Use represents the percentage of occurrence in the scats.

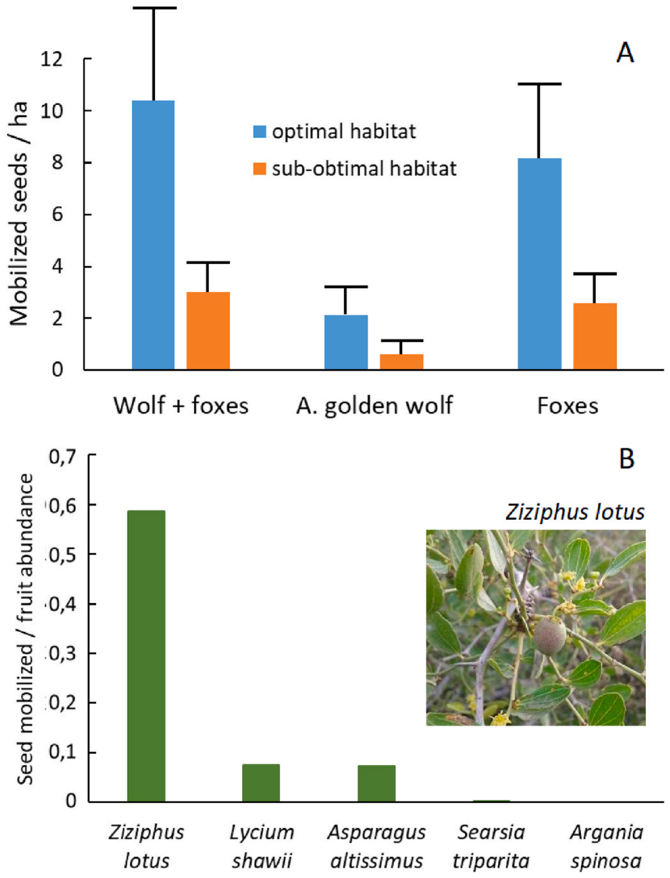

Fig. 4. A) Estimated number of seeds dispersed by canids in the North Atlantic Sahara Desert. Optimal habitats represent oueds and secondary ravines; sub-optimal habitats present rocky areas. B) Dispersed seeds/available fruits rate within optimal habitats.

4. Discussion

We have confirmed the role of certain carnivore species as potential seed dispersers in the Sahara Desert, although this role was limited to three species within the local mammalian community. Out of the twelve detected carnivore species, only African golden wolves, red foxes and Rüppell's foxes were able to disperse seeds into the proposed optimal macro-habitats (areas where conditions may enhance germination and subsequent seedling survival). Other species either do not consume fruits, such felids (see results for the North African wildcat) and likely the Saharan striped polecat (Larivière et al., 2009), or we were not able to detect sufficient scats. The latter is the case for common genets, a viverrid known to frequently consume fruits (Virgós et al., 1999). In our study area, however, we observed the scats of genets in latrines placed in rocky areas, a behavior that severely limits their potential role as seed dispersers. This was also the case for honey badgers, a mustelid that consumed *P. dactylifera* dates, but deposited seeds in suboptimal sites for recruitment (i.e., micro-habitats near water sources, such as oases in the study area).

Due to their trophic plasticity and large home ranges with frequent long-distance movements, canids play a key role in seed dispersal within several multiple habitats (Spennemann, 2021), including the semi-arid regions of Southern Africa (Kamler et al., 2020). Of the four canid species inhabiting the Sahara Desert, we were unable to confirm the fennec fox as a seed disperser, primarily because we only found three scats (that lacked seeds). This Saharan endemic canid can consume fruits (Karssene et al., 2019), with palm dates being particularly relevant in southern

Algeria (Brahmi et al., 2012). In our study area, we detected a relatively high abundance of fennec fox within the regs habitats (Gil-Sánchez et al., 2024). However, this type of habitat largely lacks the target plant species in this region, suggesting that the local role of fennec foxes in seed dispersal is likely marginal at best. A similar situation may apply to Rüppell's fox, the most abundant carnivore species in the regs (Gil-Sánchez et al., 2024). This small fox is detected at very low abundance within the djebels after rainy periods, and is absent during short-term droughts, due to the competitive exclusion exerted by the larger canids (Gil-Sánchez et al., 2024). However, the role of the Rüppell's fox could be more important in the Atlantic Sahara regions south of our study area, where red foxes are absent (Olson et al., 2001).

The frequency of occurrence of the fruits to the local diet of African golden wolves was similar that reported in other Saharan areas (28.7 - 33.5% frequency of occurrence (FO) in Tunisia (Karssene et al., 2019) but lower than in the more productive Mediterranean habitats (63% FO; (Eddine et al., 2017). For red foxes, fruits typically represent a large portion of the diet in non-arid ecoregions (see e.g. (Soe et al., 2017)), though the contribution in southern Tunisia (9.5 – 17.89% FO (Mudappa et al., 2010)) is not very different from what we observed. It is important to highlight that the second period of our study (2017-2018) was conducted during a local drought period that impacted not only the vegetation of the whole region but also the abundance of African golden wolves and foxes (see details in (Gil-Sánchez et al., 2024)). While one might expect increased frequency of occurrence of fruits during rainy years due to greater fruit production, our data suggest otherwise, as the FO of fruits apparently increased during the drought period (see Table 1 for wolves and foxes). Conversely, seed dispersal rates linked to carnivore abundance would be expected to rise following rainy periods, which lead to higher carnivore populations (Gil-Sánchez et al., 2024). Therefore, long-term studies are essential to better understand the complex interactions between fruit availability, carnivore abundance, and their combined effects on seed dispersal.

We detected interspecific differences in fruit selection patterns, a behavior that directly affects seed dispersal dynamics and subsequent plant recruitment. The African golden wolf showed a strong preference for *Z. lotus* drupes, the largest and most nutritious local fruit after the highly caloric date palm drupes (Virgós et al., 1999). This drupe is also consumed by African golden wolves in the pre-Saharan regions of southern Tunisia (Karssene et al., 2019), whereas in the semi-arid southeast of Spain, the red fox acts as the main disperser (Cancio et al., 2016; Eddine et al., 2017). Scientific evidence suggests that the consumption of *Z. lotus* by foxes serves as an effective mechanism of endozoochorous dispersal, with high germination rates of viable seeds retrieved from faeces (Cancio et al., 2016). Thus, the African golden wolf may serve as a key primary disperser of *Z. lotus*, contributing to the natural regeneration of this arborescent shrub in the Sahara, and potentially in other North Africa ecoregions where the species is more abundant. Interestingly, the marginal contribution of *Z. lotus* in the diet of foxes in our study area could reflect the effects of intra-guild competition. The smaller foxes may avoid a resource that is strongly preferred by the larger African golden wolf. Both species appear to overlap spatially at third and fourth order habitat selection levels (Gil-Sánchez et al., 2024) and therefore would have similar access to *Z. lotus* plants. Since wolves prey on foxes in the area (Gil-Sánchez et al., 2024) foxes may reduce predation risk by limiting their consumption of *Z. lotus* drupes. Foxes showed a strong selection of *L. shawii,* a Solanaceae with small subglobose berries, orange or reddish in colour, shiny when ripe, and with a high sugar content, all traits that makes it highly attractive to foxes (Herrera, 1989). The few available scientific references regarding the seed dispersal of *L. shawii* cited lizards and geckos as dispersers (Nogales et al., 1998; Valido and Nogales, 1994), however our results, along with data from southern Tunisia (Karssene et al., 2019), suggest that African golden wolves and red foxes (and possibly also Rüppell's foxes) could play an important role as well. Foxes also selected asparagus fruits, a globose berry also consumed and dispersed in Australia (O'Connor et al., 2019). However, its contribution to the Saharan diet of Rüppell's and red fox is relatively low, indicating a limited contribution to seed dispersal.

Other local plants were rarely consumed by carnivores despite their highly attractive features according to (Herrera, 1989), especially palm dates, *N. retusa* fruits and *S. tripartita* drupes. During the second part of the study, the availability of dates was zero, and *N. retusa* plants were absent in the surveys, but *S. tripartita* drupes were by far the most abundant fruit. The low presence of this species in the diet of the African golden wolf contrasts with the results provided by (Valverde, 1957) in the southern Atlantic Sahara, where they reported 85.4% FO of drupes of *S. tripartita* in 55 African golden wolf scats. This information may highlight some limitations of our short-term study, indicating that further research is necessary, particularly during rainy periods when primary productivity peaks. The argan tree is another interesting case of a non-consumed fruit despite its high abundance, especially in the djebel Ouarkziz during the winter season. The only existing scientific references on the consumption of argan fruits point to ungulates, particularly domestic livestock, as the primary dispersers of its seeds; they consume approximately 47-84% of these fruits during the driest months (Okia, 2010). Additionally, they contribute to seed dispersal by regurgitating the seeds during rumination rather than defecating them. To our knowledge, this is the first study to examine the relationships between this endemic Moroccan tree and local carnivores, revealing that the fruits are not attractive to them. The pulp of the argan fruit contains chemicals compounds that makes its flavour extremely bitter (Charrouf et al., 2007) and does not align with the selection criteria proposed by (Herrera, 1989) and (Debussche and Isenmann, 1989).

The rates of dispersed seeds deposited in optimal environments (at the landscape level) for germination suggest a key role of canids as dispersers of the targeted plant species in the Saharan ecoregion, especially for *Z. lotus*. The alternative zoochorous dispersal agents for this group of scrubs and trees in such an arid environment include ungulates, rodents, lagomorphs, small birds, and reptiles. The study area is inhabited by three species of wild ungulates: the Cuvier's gazelle (*Gazella cuvieri*), dorcas gazelle (*G. dorcas*), and Barbary sheep (*Ammotragus lervia*) (Aulagnier et al., 2017), but due to poaching, their current abundance is probably too low for effective ecological function, while no seeds of the nine targeted species were detected in the diet of one of them, the Cuvier's gazelle (Herrera-Sánchez et al., 2023). In addition to the aforementioned goats, dromedaries are common in the region, although their potential role in the dispersal of the targeted plants is very low (Chehma et al., 2023). We detected five species of rodents coexisting with the target plants in the study area (data from systematic remote camera surveys, (Gil-Sánchez et al., 2024), and Sherman's traps surveys): one ground squirrel (*Atlantoxerus getulus*) and four medium-sized (*Meriones* sp.) to small-sized dormice (*Elyomis munbianus*; only one record) and two gerbil species (*Gerbillus* sp.). The frequent dual role of rodents (seed predation versus dispersal) limits the effectiveness of mutualistic synzoochorus dispersal (see (Yu et al., 2023) for a desert ecosystem), while lagomorphs (one species: *Lepus saharae*, data from this study) might consume only the pulp (Cancio et al., 2017). However, rodents and reptiles could disperse more seeds of the target plant species, as they are more abundant than carnivores in our study area. In all cases, the dispersal distance achieved by these animals is considerably shorter than those of carnivores (Draper et al., 2022; Virgós et al., 1999) this is also true for reptiles, with 5 small lizard species, 7 gecko species and 3 agamids (Bons and Geniez, 1996), which might be important for dispersing small berries within patches. Regarding birds, 3 sedentary and 5 wintering Turdidae and Sylviidae species (Bergier et al., 2022) probably play a key role in dispersing smaller berries (*L. shawii, S. tripartita, N. retusa*), since this sweet, small fruits are heavily consumed by these taxa, playing an important dispersal role elsewhere. However, they are unable to ingest the larger seeds of *P. dactylifera* and *Z. lotus* drupes. For these two plants, only carnivorans and the brown-necked raven (*Corvus ruficollis*) due to its large size would be able to ingest the seeds in the study area, but ravens are much less abundant than wolves and foxes (per. obs. J. M. Gil-Sánchez & I. Cancio). In any case, it is necessary to carry out research on the functional complementarity of all these groups in the Sahara Desert.

One limitation of our study is the lack of knowledge regarding the post-dispersal demographic processes in the plant life cycle (seed survival and germination, seedling establishment, etc. (Wang and Smith, 2002);). Regarding seed viability, it is well-studied that the pulp removal and seed scarification that occur when canids consume fruit can improve germination rates or increase seedling quality compared to non-consumed seeds (Escribano-Avila, 2019; Spennemann, 2021; Burgos et al., 2024), although results may vary depending on the fruit species (Cypher and Cypher, 1999). Another limitation of the study is that we did not consider microsites within a habitat deemed optimal (oued/ravine) in our analyses. Microsites are important for understanding whether the seedling that germinates has a higher or lower chance of survival (Spennemann, 2021). In particularly arid and even semi-arid areas, the presence of adult nurse plants is essential, as they offer protection during the early stages of growth (Tirado, 2003).

5. Conclusions

This study provides the first evidence of the role of carnivores as seed dispersers in the Sahara Desert, an ecoregion that remains poorly understood in terms of plant-animal ecological functions and interactions. The attention given by wildlife researchers to this vast desert remains strikingly limited, largely due to severe limitations that impact any attempt, such as remoteness, logistical challenges, and security concerns arising from regional conflicts (Brito et al., 2016). Despite these obstacles, this study was successfully conducted, though we acknowledge the limitations posed by a relatively small sample size. Nonetheless, our findings offer empirical support for the role of canids as seed dispersers in this ancient, hyper-arid ecosystem. Additionally, we found compelling evidence suggesting that intra-guild competition influences seed dispersal patterns. Our study represents only a first step toward understanding this vital ecosystem service provided by carnivorans in the Sahara Desert. Future research will be necessary to evaluate dispersal distance, post-dispersal stages, such as seed germination, seedling establishment, and survival success across different microhabitats within each macrohabitat. Further research is needed, not only to overcome the limitations previously discussed, but especially to support long-term monitoring efforts capable of capturing the full range of interannual rainfall heterogeneity, from extended droughts to typical primary production after rainfall events.

CRediT authorship contribution statement

Inmaculada Cancio: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Joaquín Pérez:** Data curation, Investigation, Visualization. **A. Javier Rodríguez-Siles:** Data curation, Validation, Visualization. **F. Javier Herrera-Sánchez:** Data curation, Investigation, Validation, Visualization. **Ángel Arredondo:** Data curation, Visualization. **Miguel A. Díaz-Portero:** Data curation, Validation, Visualization. **Jose Manuel Martín:** Data curation, Visualization. **Gerardo Valenzuela:** Data curation, Visualization. **Mariola Sánchez-Cerdá:** Data curation, Validation, Visualization. **Thomas Lahlafi:** Data curation, Visualization. **Abdeljebbar Qninba:** Project administration, Validation, Visualization. **Emilio Virgós:** Investigation, Methodology, Supervision, Validation, Visualization. **Jose María Gil-Sánchez:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Supervision, Validation, Visualization, Writing – review & editing.

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.

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Data availability

Data will be made available on request.

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