



Hares (*Lepus* spp.) as seed dispersers of *Retama raetam* (Fabaceae) in a sandy landscape

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Hares in the sandy ecosystem of the Mediterranean coastal plain in Israel consume pods of the widespread desert plant *Retama raetam*. The aim of this study was to explore some of its qualities as a dispersal agent of such an important component of the vegetation of Mediterranean arid habitats. Although the pericarp acts as the nutritious 'reward', the hares do not select the most profitable pods with the highest pericarp/seed mass ratio. Of the 718 randomly collected hare pellets 43% contained *R. raetam* seeds. More than half (55%) of those containing seeds had only one seed, 43% contained two to three seeds and the other 2% contained four to five seeds. Seeds from hare pellets imbibed water more slowly than either exposed seeds which were collected from the sand surface, or manually scarified seeds, but faster than intact seeds which were removed from pods. Untreated seeds from pods had low germination (6%), but most were alive, as indicated by high (70%) germination when scarified. While only 6% of seeds obtained from hare pellets germinated, 44% of them germinated after scarification. Thus, hares did not have a lethal effect on seed viability. It should be emphasized that the difference between these two values (38%) is added to the soil seed bank as 'exposed seeds'. The height and growth rate of seedlings that emerged from hare pellets in pots did not differ from those of seedlings receiving other treatments. Hence, the hypothesis that seedlings in pellets may be favoured by the nutrient pool available to them was not confirmed. We conclude that hares have the potential to act as a legitimate dispersal agent for *R. raetam*, especially as a carrier of seeds away from the parent plant.

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Keywords: *Retama raetam*; seed germination; endozoochory; food selection; pericarp:seed mass ratio; hardseedness

Introduction

Propagule dispersal in plants is a trade-off between the advantages of locating new or under-exploited habitat patches and the dangers of abandoning a site at which some degree of reproductive success has been achieved (Zedler & Black, 1992). Many desert plants have adaptations that hamper seed dispersal (Zohary, 1962; Ellner & Shmida, 1981). This could be interpreted as adaptations to reduce high mortality due to seed

dispersal in areas where most surroundings are hostile and favourable sites are rare (Ellner & Shmida, 1981). Therefore, the importance of seed dispersal by animals which consume fruits (endozoochory) tends to decline in dry habitats (Howe & Smallwood, 1982) and is relatively rare in coastal strand, Mediterranean and desert climates (Carlquist, 1974; Ellner & Shmida, 1981). Nevertheless, endozoochory does occur in 3% of the true desert plants in Israel (Ellner & Shmida, 1981).

Seed germination and seedling establishment are the most critical stages in the plant life cycle (Mayer & Poljakoff-Mayber, 1989). Germination is a risky, irreversible transit between the life phase most tolerant of drought to one most susceptible to it. Seeds that have an impermeable seed coat, and thus are unable to hydrate and to germinate even when in contact with free water, are defined as 'hard seeds' (Kigel, 1995). This seed trait is common in the Fabaceae and among other plant families typical of arid and semi-arid zones (Rolston, 1978). Twenty-one annual species of legumes growing in the arid part of Israel were found to be hardseeded (Koller, 1969). Legume seeds have a hylum that acts as a one-way hygroscopic valve, allowing seed dehydration in a dry environment but no hydration in a humid one (Hyde, 1954). As a result, these seeds can maintain the lowest water content reached after shedding, 4–6% in a typical Mediterranean summer. This low water content may extend the life-span of seeds in the seed bank (Kigel, 1995). Extreme diurnal temperature fluctuations on the soil surface during the hot Mediterranean summer may cause the breaking of hardseedness and germination the next winter (Kigel, 1995). The combination of hardseedness and endozoochory seems to be rare, and most literature on the effect of animals on the dispersal and germination of this kind of seed has focused on *Acacia* sp. (e.g. Hauser, 1994; Miller, 1994).

We studied the relationships between *Retama raetam* (Forssk.) Webb, one of the most important plants in the east Mediterranean deserts, and hares (*Lepus* spp.). The Mediterranean coastal plain of northern Israel, in spite of its typical Mediterranean climate, has little actual water available for plants due to the low field capacity of the sand. Therefore, this ecosystem supports many Saharo-Arabian species such as *Artemisia monosperma* Delile, *Helianthemum stipulatum* Forssk., and abundant *Retama raetam* (Zohary, 1962; Danin & Plitmann, 1987).

Retama raetam (Fabaceae) is a glabrescent large shrub growing mainly in the Saharo-Arabian deserts, and is also a dominant component of the stable or semi-mobile sands of the Mediterranean coastal plain (Kutiel *et al.*, 1979/80). It bears tiny leaves on the current growing branches in winter, but is leafless during the long and dry summer. Flowering occurs during February–March, and the fruits are ripe by the end of spring. The indehiscent fruit is a pod with a tapering tip, with a leathery, horny or parchment-like pericarp. Most of the newly matured *R. raetam* pods fall off by the beginning of summer (June). The fallen pods, including the seeds, are then consumed by mammals such as hares (*Lepus* spp.) and goats (Gutterman, 1993).

Previous studies have emphasized the role of rabbits as dispersers by endozoochory, especially of small (< 1.0 mm) seeds (e.g. Staniforth & Cavers, 1977; D'Antonio, 1990; Zedler & Black, 1992; Malo & Suárez, 1995; Malo *et al.*, 1995; Nogales *et al.*, 1995). However, no information is available on the role of hares, the second important genus in the Lagomorphs, in seed dispersal. Two species of hares (*Lepus capensis* L. and *L. europaeus* Pallas) inhabit the coastal plains of Israel. *Lepus capensis* has a vast geographic range including northern, eastern, and southern Africa, the Mediterranean basin including Israel, Arabia, Iran and northern China (Chapman & Flux, 1990). *Lepus europaeus* populates most of Europe up to 60° N and has been introduced to the Mediterranean as well (Chapman & Flux, 1990). Hare density in Israel was estimated as varying from one to 10 individuals per km² in desert and agricultural lands, respectively (Mendelson & Yom-Tov, 1987).

In this paper we assess several aspects of the potential role of hares as seed dispersers of *R. raetam* through the following questions: (1) do hares select pods that contain

seeds of particular size (mass and length)? (2) What is the proportion of pellets that contain seeds? (3) May hare pellets containing many seeds increase the probability of intraspecific sibling competition? (4) How does seed passage through the digestive tract affect seed coat sculpture and water permeability? (5) How does it affect seed germination ecology (start, rate, and final percentage)? (6) Does the nutrient content of the faecal pellet benefit the first stage of seedling establishment?

Materials and methods

Study area

The study site was part of the coastal plain of Israel, 1 km north of Hadera river and 1 km east of the Mediterranean coast (32°29' N 34°75' E), including stabilized and semi-mobile dunes. The climate is typical Mediterranean, with cool, rainy winters (December to February) and hot dry summers (June to September). Mean temperatures of the coldest month (January) are 12–14°C and mean temperatures of the warmest month (August) are 24–26°C. Mean annual precipitation is 500–600 mm and mean annual potential evaporation 120–140 mm. Annual mean (of daily mean) of relative humidity is 70–75% with no prominent difference between summer and winter (New Atlas of Israel, 1985).

Pod, seed and pellet collections and measurements

Ripe *R. raetam* pods were collected from randomly selected plants in May–June 1992. Each pod ('intact pods') was weighed and the seeds ('intact seeds') were taken out, counted, weighed, and their length and width measured. Hare pellets ('intact pellets') and exposed seeds from the sand surface ('exposed seeds') were also collected > 10 m away from the nearest adult *Retama* plant. All pods, seeds and pellets were stored in a dry place at room temperature.

Each pellet was also weighed, and the seeds ('pellet seeds') were extracted, weighed and measured for length and width. Intact pellets with seeds were used for germination trials. Seeds could be seen in the pellets with superficial exploration.

Additional collection of exposed seeds and pellets containing seeds was carried out in July 1996 at the same site (for scarification trial).

Scanning electron microscope

Dry seed coats of randomly selected 'scarified', 'exposed' and 'pellet' seeds were examined with a scanning electron microscope (Jeol, JSM-840). The seeds were gold-coated in a vacuum (Polaron SEM coating system), photographed and compared.

Water imbibition

Twenty 'intact', 'intact scarified', 'exposed' and 'pellet' air-dried seeds were wetted in a bath of distilled water at room temperature. 'Intact scarified' seeds were seeds rubbed with sandpaper until the seed coat was completely worn through at any point. At intervals of 1–2 days for 61 days the seeds were removed from the water, dried with tissue paper, and individually weighed. In a preliminary study the imbibition of water was followed at intervals of 2 h for 24 h, but none of the seeds imbibed water during that period. Germinated seeds were removed from the experiment.

Germination and first stage of establishment

Germination experiments were performed in autumn 1992 in pots (12 cm in diameter) containing washed sand, in a semi-shaded non-heated and ventilated greenhouse. Pots were kept moist all the time by automatic water mist spraying for 2 min h⁻¹. Ten 'intact pods' and 10 'intact', 'exposed' and 'intact scarified' seeds were sown in each pot in 10 replicates, and 10 'pellet seeds' were sown in pots in 34 replicates. Ten 'intact pellets', each with one seed, were sown in each pot in 20 replicates. The germination criterion was the opening of cotyledons. Germinated seeds were recorded and their height was measured every 3 days over a 165-day period. Mean seedling height of all surviving individuals was used to indicate plant performance after this period (e.g. Loiselle, 1990).

A complementary germination trial of 'exposed' and 'pellet seeds' was carried out in August 1996 in a germination chamber at 20°C with 10 h of light and 14 h of darkness. Seeds from each group were sown without any treatment and after scarification, as described. Nine seeds were sown in 10 cm Petri dishes, in 10 replicates, on filter paper with 2 ml of distilled water and kept wet. The criterion for germination was the emergence of the radicle and germinated seeds were removed. Germination was monitored every 6–8 days for 5 weeks until no more new seedlings emerged.

One-way analysis of variance (ANOVA) was used to detect differences in percentage germination (arcsin square root transformed) and seedling height among treatments on the last day of the trial. The cumulative percent germination was calculated and drawn in order to demonstrate differences in germination patterns among treatments. The quantitative evaluation of seed germination was based on two additional parameters: germination start (GS) and germination rate (GR). Germination start (GS) was defined as the time interval (days) between sowing and emergence of $\frac{1}{6} \times P$ of the seedlings when P is the final germination percentage. Germination rate was calculated by the equation $GR = (\frac{5}{6} \times P) / (T_2 - T_1)$, when T1 is the time interval (days) between sowing and emergence of $\frac{1}{6} \times P$ of the seedlings, and T2 is time interval (days) between sowing and emergence of $\frac{5}{6} \times P$ seedlings.

Results

Intact R. raetam pod and seeds

The average mass of *R. raetam* pods was 0.24 ± 0.08 g (range 0.10–0.52 g, *N* = 101). Each pod contained one to four seeds (average 1.6 ± 0.78, *N* = 131). Average seed length and width were 5.61 ± 0.67 mm and 4.68 ± 0.40 mm, respectively, and average seed mass was 0.073 ± 0.017 g (*N* = 115). A significant multiple regression equation ($F_{3,79} = 9.92$, $r^2 = 0.27$, $p < 0.0001$) was found between pod mass (dependent variable) and these three variables:

$$\text{pod mass} = -0.025 \times \text{seed mass} - 0.018 \times \text{seed length} + 0.127 \\ \times \text{seed width} - 0.249$$

The number of seeds per pod was not used as an independent variable in this equation since we intended to use this equation for predicting pod mass from seeds found in pellets. Obviously, it was impossible to identify the original number of seeds in a pod for seeds which were found in pellets. A negative correlation was detected between the number of seeds per pod and seed mass ($r_s = -0.39$, $p < 0.001$, *N* = 115).

Although the average total seed mass was about 50% of total pod mass, the maximum difference between the proportion of the pericarp (the edible part of the pod) from total pod mass and the proportion of the total seed mass from total pod mass was found in medium-sized pods (0.3 g; Fig. 1). Small and large pods contained

a relatively large mass of seeds and therefore had much less available pericarp relative to seed mass and were expected to be much less profitable to hares (Fig. 1).

Hare pellets

Of the 718 randomly collected hare pellets, 42.5% contained *R. raetam* seeds. Pellets without seeds were significantly lighter than those that contained seeds (0.21 g and 0.27 g, respectively; $T_{669} = 11.26$, $p < 0.0001$). More than a half (55%) of the seeds containing pellets had only one seed, 43% contained two to three seeds and the remaining 2% contained four to five seeds. A positive correlation was found between pellet mass and the number of seeds per pellet ($r_s = 0.49$, $p < 0.0001$, $N = 671$). The total seed/pellet mass ratio was between 0.31 and 0.52 for pellets containing one and five seeds, respectively.

Seeds obtained from hare pellets were not significantly different in their mass average (0.073 g, $N = 132$) from 'intact seeds' and from 'exposed seeds' (0.076 g, $N = 100$; $F_{2,344} = 1.13$, $p > 0.05$). Seeds removed from pellets were also similar in their average length (5.63 mm, $N = 132$) to 'intact seeds' but slightly smaller than the 'exposed seeds' (5.83 mm, $N = 100$; $F_{2,344} = 4.36$, $p < 0.05$). No difference in seed width was detected among these three seed types ($F_{2,344} = 1.84$, $p > 0.01$).

The above multiple regression equation for pod mass was used to calculate the average pod mass taken by hares according to mass, length and width of seeds found in pellets. The average consumed pod was 0.23 g (Fig. 1), which was slightly lighter than the average pods mass found in the area (Fig. 1) and also lighter than the most

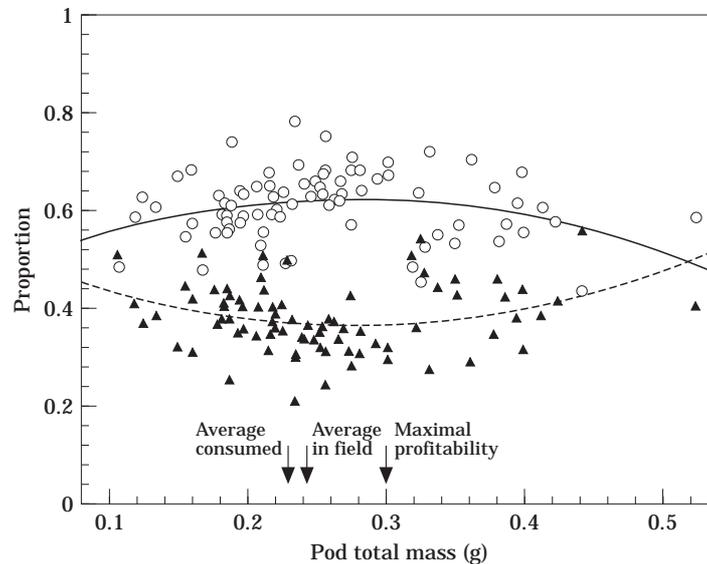


Figure 1. Relationships between total pod mass and the proportion of total seed mass in total pod mass (▲), and the proportion of the pericarp mass in total pod mass (○) in *R. raetam*. The lines represent the best fitted second-degree polynomial curves drawn by the linear least squares method. The equations were: $\pm 2.11X^2 - 1.17X + 0.53$. The difference between the two lines represents the expected profitability for pod consumers. Maximal profitability was found in 0.3 g pods, while average pod mass in the field was 0.24 g. The average pod mass that hares consumed was 0.23 g (calculated by multiple regression equation for pod mass from mass, length and width of seeds found in hare pellets — see Results).

profitable pod which had the maximum relative difference between pericarp mass and total seed mass (Fig. 1).

Furthermore, Chi-square test showed that the distribution of seed mass in pellets grouped into six classes (< 0.05, 0.05–0.06, 0.06–0.07, 0.07–0.08, 0.08–0.09, > 0.09 g) were not significantly different from the distribution of seed mass collected at random in the field ($\chi^2 = 2.63$, $p = 0.76$, $N = 246$). The same phenomenon was found with regard to seed length grouped into five classes (< 5, 5–5.5, 5.5–6, 6–6.5, > 6.5 mm; $\chi^2 = 6.94$, $p = 0.14$, $N = 216$).

The effect of hare ingestion on the sculpture of seed coat

Retama 'intact seed' surface consists of ridges and grooves (Fig. 2(a)). Passage of seeds through the digestive tract of hares narrowed these ridges (Fig. 2(b)), while in 'exposed seeds' the outer cuticular layer was removed and deep cracks in the testa were visible (Fig. 2(c)).

Water imbibition of seeds

Most of the 'intact scarified seeds' (80%) imbibed water during the experiment while only 60% of the 'exposed seeds' (collected from the sand surface), 15% of the 'pellet seeds' (removed from hare pellets in the field) and 5% of the 'intact seeds' (removed from pods) imbibed water. 'Intact scarified seeds' began to imbibe water, as indicated by their mass increase, 24 h after the experiment was set. They doubled their mean mass in 2 days and reached their mean maximal mass (161% above their original mass) in 5 days. 'Exposed seeds' began increasing their mass only after 8 days and reached their mean maximum mass (90% above original mass) after 24 days. 'Pellet seeds' began to absorb water after 38 days and reached their mean maximum mass (21% above original mass) after 40 days. 'Intact seeds' demonstrated a very low imbibition and increased their mean mass by only 15% after 57 days.

Seed germination

'Intact scarified seeds' germinated first, and had the highest germination rate and total germination percentage (Table 1). Total germination percentage was significantly different among treatments ($F_{6,98} = 34.39$, $p < 0.0001$; see also Table 1). 'Exposed seeds' germinated 1–2 weeks later, had 9–12 times slower germination rate (GR) and reached half of the total germination percentage relative to 'intact scarified seeds' (Table 1). Seeds in the other four treatments had a much lower germination rate and a low total germination percentage ($\leq 6\%$; Table 1). However, their germination start (GS) was different, where seeds in sowed fruits germinated the latest and seeds in sowed pellets germinated relatively fast (Table 1). 'Intact seeds' and 'pellet seeds' had a relatively similar GS, GR, and total germination percentage.

In the complementary trial the final germination percentage of unscarified and scarified seeds of both 'exposed' and 'pellet' seeds (Fig. 3) was significantly different ($F_{3,36} = 39.209$, $p < 0.0001$). Forty-four percent of the non-germinated 'pellet seeds', but only 30% of the non-germinated 'exposed seeds', were vital, but the difference was not significant (Fig. 3). Taking into account that 30% of the seeds in pods were already dead, the hare actually killed 26% of the ingested seeds. Germination of unscarified 'exposed' and 'pellet' seeds in the complementary trial (Fig. 3) was much lower than in the first trial (Table 1).

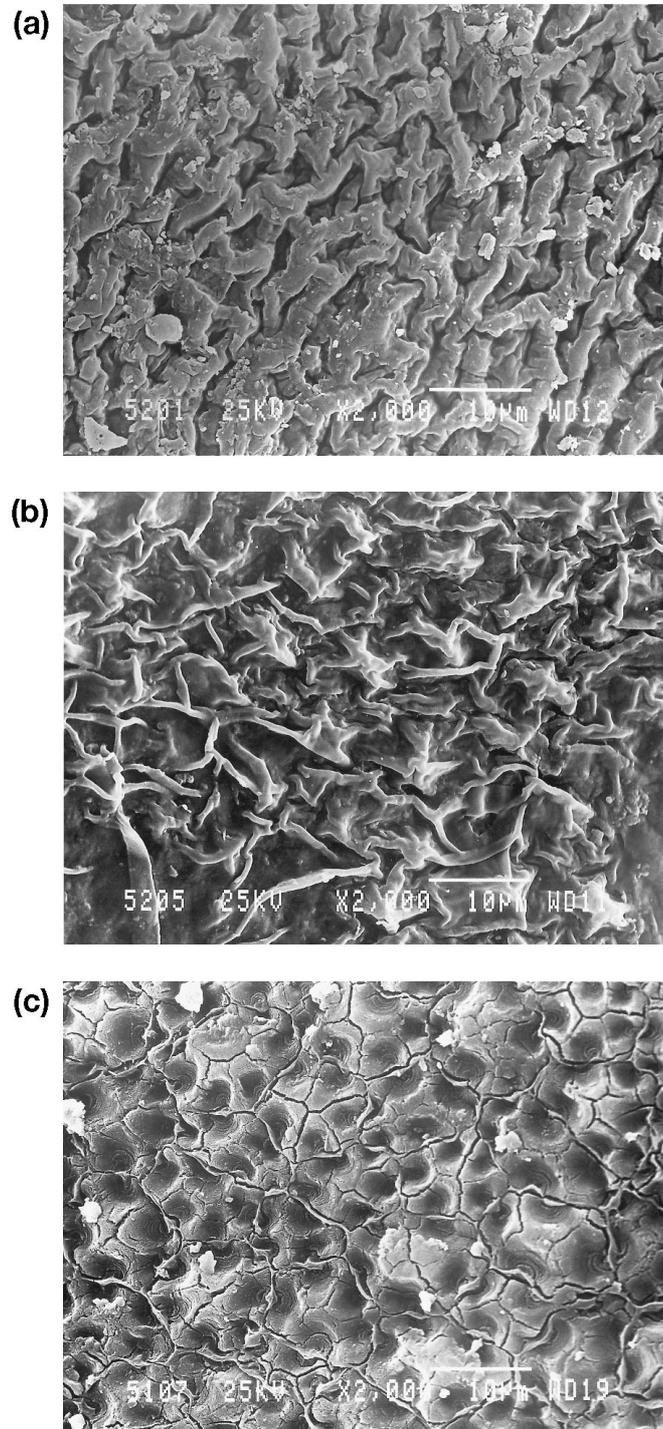


Figure 2. SEM ($\times 2000$) photographs of (a) 'intact seeds', (b) 'pellet seeds', and (c) 'exposed seeds'. Bar = 10 μm .

Table 1. Average germination start (GS, time interval in days between sowing and emergence of $\frac{1}{2} \times P$), germination rate (GR, % germination per day), and total germination of *Retama raetam* seeds. Mean height 165 days after sowing and growth rate of seedlings in pots from GS is also given. Significant differences in total germination (arcsin square root transformed proportions), seedling height and growth rate among the seven treatments ($p < 0.05$, using Duncan test) are indicated by the superscripts a-c ($a > b > c$)

Treatment (N)	GS (days)	GR (% day ⁻¹)	Total germination (%±S.D.)	Average seedling height (cm±S.D.)	Mean growth rate (cm day ⁻¹ ±S.D.)
Intact scarified seeds (10)	3	5.2	70.0±17.0 ^a	25.1±3.0 ^a	0.15±0.02 ^{bc}
Exposed seeds (10)	44	0.58	33.0±12.0 ^b	23.6±4.9 ^{ab}	0.20±0.04 ^b
Intact pods (10)	100	0.09	6.0±5.0 ^c	20.5±2.1 ^{ab}	0.32±0.03 ^a
Intact seeds (10)	53	0.05	6.0±7.0 ^c	21.5±6.4 ^{ab}	0.19±0.06 ^b
Intact pellets (20)	35	0.03	5.5±7.6 ^c	16.3±5.8 ^b	0.13±0.04 ^c
Pellet seeds (34)	47	0.04	5.6±10.0 ^c	17.9±5.5 ^{ab}	0.15±0.05 ^{bc}

Seedling height in pots

One-way ANOVA revealed that seedling height in pots, 165 days after sowing, was significantly different among treatments ($F_{6,43} = 3.05$, $p < 0.05$) but a multiple comparison test demonstrated that only the seedlings which germinated from scarified seeds (8.8 cm) were significantly higher than those which germinated from seeds in sowed pellets (Table 1). This difference was probably due to the effect of earlier germination (Table 1) and thus a longer growth period when final measurements were taken.

Growth rate of seedlings that emerged from 'pellet seeds' was similar to most other treatments (Table 1). The significantly higher growth rate of seedlings that emerged from 'intact pods' was probably due to their late germination in a relatively warm season.

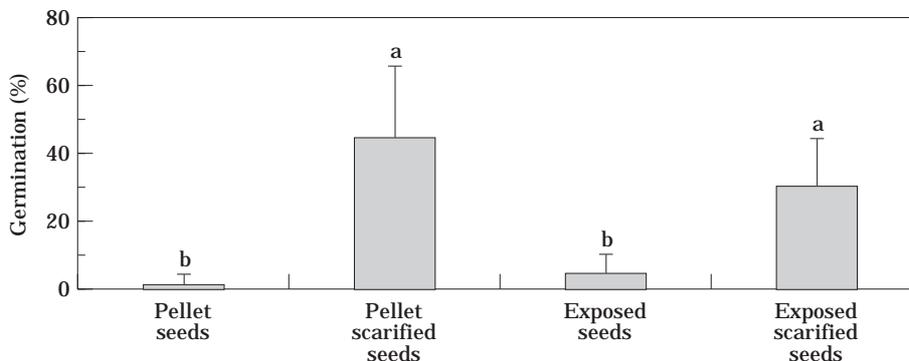


Figure 3. Mean germination (+ S.D.) of scarified vs. non-scarified seeds either removed from hare pellets ('pellet seeds') or collected from sand surface ('exposed seeds'). Significant differences in mean germination (arcsin square root transformed proportions) among the four treatments ($p < 0.05$, using Duncan test) are indicated by different letters above bars.

Discussion

Typical endozoochorous fruits have a fleshy pericarp and are eaten by fruit-consuming animals (van der Pijl, 1972). Grazing animals serve as dispersers mainly for range and meadow plant species with small dry fruits and small digestion-resistant seeds, which are ingested during the grazing activity rather than selected actively (Lehrer & Tisdale, 1956; Thomson *et al.*, 1990; Gardner *et al.*, 1993). Dispersal of *R. raetam* seeds by endozoochory is unique in that its dry fruits are actively foraged, and thus it belongs to a special group of perennial legumes like *Acacia* spp. (Miller, 1994), *Prosopis* spp. (Peinetti *et al.*, 1993) and *Ceratonia siliqua* L. (Ortiz *et al.*, 1995).

The dispersal process may be divided conveniently into three stages: intake, transportation and deposition; each stage may be critical in determining the ultimate fate of the dispersed seeds. Thus, the overall quality of the hare as a seed disperser for *R. raetam* is a consequence of several attributes characterizing each stage.

The intake stage

The large proportion of pellets containing *Retama* seeds (> 40%) indicated that the pods were actively collected and that this food item is an important part of the hares' diet during the fruiting season. Although the pericarp acts as the nutritious 'reward', hares did not select the most profitable pods with the highest pericarp/seed mass ratio but consumed pods of average size. These pods also contained seeds of average size. Moreover, the distribution of seed size (mass and length) in pellets represented the distribution of seeds in the *R. raetam* population in the field. Thus, it seems that hare diet is based on opportunism, and despite their role in the dispersal of *R. raetam* seeds, hares probably do not currently act as a selective force in shaping *R. raetam* pods and seeds to a different (small or large) particular size. This is in agreement with Janzen's (1983) notion that fruits should be particularly conservative with respect to animal dispersal agent relationships.

Internal transport and germination

Germination rate of intact *Retama* seeds is very low (see also Gutterman, 1993) because the impermeability of the seed coat prevents imbibition (Kigel, 1995). Mechanically scarified seeds quickly imbibed water and reached very high germination percentages (70%), which means that most seeds in pods were capable of germination when the tegument was broken. In nature the hard seeds of *R. raetam* become permeable due to scarification by the siliceous sand, chemical and mechanical changes within the hare intestines, and mainly due to extreme daily temperature cycles. Heat may rupture the seed coat, as reported for many plants (Tran & Cavanagh, 1984) and especially of legumes (Kigel, 1995). Daily alternations of temperature were found to be effective when the high temperature in the daily cycle was above 45°C (Taylor, 1981).

Retama pods were never observed at a distance from mother plants. Their seeds are round shaped and relatively heavy and are not transported by winds. Furthermore, seed-containing pellets of other potential dispersers were not found (pers. obs.). Therefore, we assume that 'exposed seeds' that were collected at a distance from parent plants were distributed by hares, and all 'exposed seeds' were earlier 'pellet seeds'. Thus, 'exposed seeds' experienced both the biotic effect of the hare intestine and the abiotic effects of sand and temperature (noon soil temperature in May–June 70–80°C, unpublished data).

Two facts support our assumption that 'exposed seeds' originated from 'pellet

seeds'. First, water imbibition by 'exposed seeds' was higher than by 'pellet seeds'. Second, the outer layer of the seed coat disappeared and cracks were present in the 'exposed seeds' but not in the 'pellet seeds', as observed in SEM photos.

Hares did not increase the final germination percentage relative to 'intact seeds'; both were < 6%. However, despite the low germination, the viability of 'pellet seeds' was 44%. It should be emphasized that the difference between these two values (38%) is added to soil seed bank as 'exposed seeds'. Thus, the hare intestine exerted no negative effect on *Retama* seed germination. These results are in contrast to other studies on viability of seeds after passage through the digestive tract of Lagomorpha (Staniforth & Cavers, 1977, but see D'Antonio, 1990; Manoz Reinoso, 1993; Nogales *et al.*, 1995), where most of the seeds were destroyed. The 44% of seeds that survived hare ingestion was much higher than the values reported for *Acacia* seeds consumed by ungulates (Miller, 1994).

Deposition of seeds

No hare pellets were observed beneath individuals of *R. raetam* (pers. obs.). Dispersal away from a parent plant by hares is one potential benefit to *R. raetam*. More than half of the hare pellets contained only one seed and > 40% contained two to three seeds. The presence of more than one seed in the pellet can influence post-dispersal fate of seeds through effects on both post-dispersal seed predation and sibling competition for resources (Janzen, 1983; Howe, 1986). Although the number of *R. raetam* seeds per pellet is relatively low, clumps of pellets in certain feeding sites (pers. obs.) would create a relatively high seed density, increasing the probability of sibling competition. Microhabitats with such high pellet and seed density may also attract predators (Janzen, 1982*a,b*). Furthermore, seeds from at least one other species (*Silene succulenta* Forssk.) were observed in hare pellets (pers. obs.). Hence, *R. raetam* seeds scattered by hares may still be exposed to intra- and interspecific competition and to pathogen, rodent and insect attacks.

It is generally assumed that seeds surviving ingestion and digestion by cattle will be deposited in a moist, nutrient-rich medium that will facilitate germination and establishment (Archer & Pyke, 1991) but no information is available concerning the effect of Lagomorph pellet microenvironment on these processes. The height of seedlings that emerged from hare pellets 165 days after sowing in pots was similar to that of seedlings which emerged from sowed seeds. Hence, the hypothesis that seedlings in pellets may be favoured by the nutrient pool available to them was not confirmed. It seems that the very small amount of dry matter in the hare pellet is unable to release the significant amount of nutrients which would be enough to influence seedling establishment.

Establishing that viable seeds are present in hare pellets is only the first step in understanding the significance of hare-mediated dispersal. Ideally, one would like to know the hare pellet seed shadow, but it is still unknown where hares choose to sit while processing and defaecating seeds. The defaecating sites and the seed shadow generated by hares are especially important in this ecosystem where dunes are shifting. Hare behaviour should be critical for the recolonization of suitable habitats and for the reproductive success of *R. raetam* in this ecosystem. Therefore, further study on the seed shadow generated by hares should reveal if its activity actually increases *R. raetam* fitness in this sandy ecosystem.

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