Frugivore carnivores: preferences and contribution to seed dispersal of red fox *Vulpes vulpes* (Linnaeus, 1758) and stone marten *Martes foina* (Erxleben, 1777) in Carrascal de la Font Roja Natural Park (Alicante, Spain)

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**Abstract**

The contribution of red fox and stone marten as seed dispersers in a Mediterranean mountain protected area is analysed. We gathered 332 scats and analysed seed content in presence and number. The eight species eaten in greater proportion were selected, three of them domesticated. Seed and plant remains are present in half of the scats found. Seed presence is distributed almost equally in summer (29%), autumn (34%) and winter (37%). The most dispersed wild species are *Juniperus phoenicea* subsp. *phoenicea*, *Rhamnus alaternus* and *Amelanchier ovalis* in a lower proportion. Red fox exploits more domesticated species, which presence in the Natural Park is lower. On the contrary, stone marten consumes more *J. phoenicea* and *A. ovalis* than red fox, but shows a certain preference for *Prunus avium* subsp. *avium*. Both carnivores might have a relevant role on long distance seed dispersal for *R. alaternus*, which is normally dispersed by birds and ants. The different exploiting rate among the plant species found compared with their presence in the area leads to think that there exist preferences in these carnivores’ feeding habits. Factors as the percentage of relative pulp weight and smell of the fruits and the habitat of the plant species could be related. Further research is needed to actually know the importance of endozoochorous seed dispersal by carnivores and determine patterns in time and preferences.

**Keywords:** dispersal, fleshy fruit, stone marten, seed, red fox

**Resumen**

Se analiza la contribución del zorro y la garduña como dispersores de semillas en un área protegida en un ecosistema mediterráneo de montaña. Se recolectaron 332 excrementos y se analizó el contenido de semillas en presencia y número. Se seleccionaron las ocho especies consumidas en mayor proporción, tres de ellas domésticas. Semillas y material vegetal están presentes en la mitad de los excrementos. La presencia de semillas se distribuye de forma equilibrada entre el verano (29%), el otoño (34%) y el invierno (37%). Las especies más dispersadas son *Juniperus phoenicea* subsp. *phoenicea*, *Rhamnus alaternus* y *Amelanchier ovalis* en menor proporción. El zorro explota más especies domésticas, cuya presencia en el Parque Natural es menor. Por el contrario, la garduña consume más *J. phoenicea* y *A. ovalis* que el zorro, pero muestra cierta preferencia por *Prunus avium* subsp. *avium*. Ambos carnívoros podrían tener un papel relevante en la dispersión a larga distancia de *R. alaternus*, que normalmente es dispersado por aves y hormigas. La diferente tasa de consumo entre las especies encontradas, comparada con su presencia en el área, conduce a pensar que existen preferencias en los hábitos alimentarios de estos carnívoros. Factores como el porcentaje relativo de peso de la pulpa y el aroma de los frutos, y el hábitat de las especies...
Introduction

Seed dispersal mediated by animals through the consumption of fruits, or endozoochory, is a deciding ecological process for some plant species whose dispersal can depend almost exclusively on it. Although endozoochory is a mixture of positive and negative effects upon the seeds (Fedriani & Delibes 2011), legitimate dispersers are generally defined as those animals which consume the whole fruit without damaging the seed and are usually more dependent on its consumption than seed predators (Herrera 2004). Many carnivorous and omnivorous mammals play this role, as they ingest large quantities and varieties of fleshy fruits in Mediterranean habitats (Herrera 1989, Willson 1993, Jordano et al. 2007). Due to their feeding habits, red foxes Vulpes vulpes (Linnaeus, 1758), stone martens Martes foina (Erxleben, 1777), badgers Meles meles (Linnaeus, 1758) and common genets Genetta genetta (Linnaeus, 1758) stand out among carnivores (Herrera 1989, Rosalino & Santos-Reis 2009).

Most of the studies on seed dispersal, usually conducted by plant ecologists, simplify this complex process by obviating the disperser behaviour (Santamaría et al. 2008). Nevertheless, these seed dispersers are among the first landscape architects, as their activity determines the diversity, abundance, and spatial distribution of seed banks (Herrera 1985). Indeed they have a strong influence on the dispersal patterns (Westcott & Graham 2000, Westcott et al. 2005, Karubian & Durães 2009), and can even determine the spatial distribution of dispersed plant species (García et al. 2007, Jordano 2007, Santamaría et al. 2008) and their population structure (Jordano et al. 2004).

Due to such complex circumstances as fragmentation or climatic change, the process of endozoochorous long-distance seed dispersal is being negatively affected in ways we still ignore, as the consequences of dispersers loss and the possible synergistic effects between environmental impacts are yet unknown (Santamaría et al. 2008). Thus, it is important to determine the contribution of endozoochory to seed dispersal.

Several studies in the area where this study was conducted (Terrones et al. 2008, Bonet et al. 2009) revealed important densities of stone marten and red fox, which may imply that endozoochory by these mammals could be relevant. This work is aimed to quantify the importance of the contribution of these two carnivores to the seed dispersal of some of the most common fleshy-fruited shrub species in the area, and show some particular preferences on the plant dispersed.

Material and methods

The study has been carried out in Carrascal de la Font Roja Natural Park (Alcoi, Alicante, SE Spain). This is a protected area consisting in a mountain range where the most relevant species is the holm oak (Quercus ilex subsp. rotundifolia (Lam.) Schwartz ex T. Morais). This species appears along with some deciduous trees as the South European flowering ash (Fraxinus ornus L.) and a subspecies of the Italian maple (Acer opalus Mill. subsp. granatensis (Boiss) Fontquer & Rothm.), with an understorey rich in fleshy-fruited shrubs.

A gathering of faeces belonging to stone marten and red fox has been conducted along a forest track 3.5 km long (Figure 1). This track runs across an area where the main ecosystems are holm oak forest and open shrub with disperse oak trees. These are two of the most representative ecosystems within the Natural Park. However, the area covered by the track may not include the vital areas of many individuals. This means that the scats found could belong to few of them and not to the whole fox and stone marten’s populations. The scat sampling was conducted between years 2010 and 2011 in the months of July, October-November, February and April-May, taking samples once every week during four weeks each season.

A total of 332 scats were gathered, 173 belonging to red fox and 159 to stone marten. Collected scats were left to dry in open air at room temperature before their storage. The samples were disaggregated with high-pressure water over a 1 mm mesh sieve. The remaining material was analysed and classified...
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in the following categories: (1) seeds of fleshy-fruited species; (2) other vegetal material (fibers, leaves, fruit remains, etc.); (3) small mammals (shrews and rodents); (4) wild boar (carcasses); (5) other mammals (lagomorphs and domesticated animals); (6) birds; (7) reptiles; (8) insects from the Order Orthoptera; (9) insects from the Order Coleoptera; and (10) other insects. Animal remnants were composed mainly of fur and fragments of bones, feathers, scales and insect exoskeletons.

The eight plant species eaten in greater proportion by both carnivores were selected for the analyses. They were classified as wild or domesticated species (Table 1). An index of presence of these plant species was estimated, based on the data of presence in squares of 1x1 km presented in Serra & Soler (2011) and completed with personal observations (unpublished data). We considered two levels: (1) the whole Natural Park with its buffer area (6,326 ha), and (2) the core area (2,298 ha), where the sampling was carried out. These data were compared with the probability of seed presence of each species in scats through Pearson’s correlation coefficient.

Seeds were identified following García-Fayos (2001). Non-predated seeds (the ones not broken) were counted. Broken seeds were eliminated. Aborted seeds that could be distinguished at a glance were also dismissed. This was possible only for *Amelanchier ovalis* Medik., *Juniperus phoenicea* L. subsp. *phoenicea* (hereafter *J. phoenicea*) and *Rhamnus alaternus* L. We found a high number of seeds from the domesticated species *Ficus carica* L., but they could not be counted accurately due to losses during sample processing. Therefore, it was eliminated from the statistical analyses based on number of seeds and only used its data of presence. The number of fruits consumed was estimated considering the mean number of seeds per fruit obtained from personal observations and from Vázquez-Yanes et al. (1999) in the case of *F. carica*.

The species *Olea europaea* L. could include here seeds belonging to the wild variety, *O. europaea* L. var. *sylvestris* Brot. Although this variety is less abundant than the domesticated one, its presence could be greater than expected (Serra & Soler 2011). *O. europaea* and *Prunus avium* L. subsp. *avium* (hereafter *P. avium*) are cultivated in the area. On the contrary, *F. carica* grows occasionally near human settlements. Some individuals of these three domesticated species can also be found occasionally growing wild in the area.

In order to study the absence of *Juniperus oxycedrus* L. subsp. *oxycedrus* (hereafter *J. oxycedrus*) in the scats, a small comparative study was carried out with fruits.
of *J. oxycedrus* and *J. phoenicea*. We compared the relative weight of the pulp of fruits of both species for trying to explain the reason why the second species mentioned is preferred over the first one.

Data have been analysed on SPSS 15.0 through a Kruskal-Wallis and Mann-Whitney’s U tests, and one-way or multivariate ANOVA when the assumptions of normality and heteroscedasticity were accomplished.

### Results

Seeds and other plant remnants appear in a high percentage of the samples of both animals (Figure 2). In most of the cases, these two categories together appear in half of the total of scats gathered or more, especially for the stone marten. Both Mann-Whitney’s U test for the stone marten (*\(\chi^2=9.533, p=0.023\)) and ANOVA for red fox (*F=20.175, p<0.001*) demonstrate that the frequency of the presence of seeds in scats is different for some of the seasons (Figure 3). In the case of the stone marten, this variable is similar in all the seasons except for spring. For the red fox, seed presence is greater in summer and autumn, followed by winter and finally spring, with much less importance.

A total of 5,133 seeds were found in the scat analysis, considering only the seven selected species. The number of seeds found in stone marten scats (*n=2,398*) and red fox’s (*n=2,871*) is similar (*\(\chi^2=90.500, p=0.160\)). Although the number of seeds of *F. carica* is underestimated, red fox disperses relatively more seeds of this species (*n=2,424; 20 scats*) than stone marten (*n=136; 3 scats*). The proportion of seeds from the other two domesticated plants is very low in both cases, 1.11% for the stone

### Table 1. List of plant species most dispersed by stone marten and red fox, and their probability of presence within the Natural Park in squares of 1x1 km, based on data from Serra & Soler (2011) and personal observations (unpublished data). The probability of presence in scats of both carnivores is also shown.

<table>
<thead>
<tr>
<th>Wild species</th>
<th>% Presence in the area</th>
<th>% Presence in scats</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Natural Park</strong></td>
<td><strong>Core area</strong></td>
<td><strong>Stone marten</strong></td>
</tr>
<tr>
<td>Snowy mespilus</td>
<td>0.24</td>
<td>0.47</td>
</tr>
<tr>
<td>(<em>Amelanchier ovalis</em> Medik.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mediterranean hackberry</td>
<td>0.18</td>
<td>0.19</td>
</tr>
<tr>
<td>(<em>Celtis australis</em> L.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phoenicean juniper</td>
<td>0.51</td>
<td>0.72</td>
</tr>
<tr>
<td>(<em>Juniperus phoenicea</em> L. <em>phoenicea</em>)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Italian buckthorn</td>
<td>0.70</td>
<td>0.86</td>
</tr>
<tr>
<td>(<em>Rhamnus alaternus</em> L.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thornless blackberry</td>
<td>0.70</td>
<td>0.70</td>
</tr>
<tr>
<td>(<em>Rubus ulmifolius</em> Schott)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Domesticated species</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common fig</td>
<td>0.13</td>
<td>0.12</td>
</tr>
<tr>
<td>(<em>Ficus carica</em> L.)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Olive</td>
<td>0.10</td>
<td>0.12</td>
</tr>
<tr>
<td>(<em>Olea europaea</em> L.)*</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wild cherry</td>
<td>0.01</td>
<td>0.00</td>
</tr>
<tr>
<td>(<em>Prunus avium</em> L. <em>avium</em>)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* This includes *O. europaea* var. *europaea* and *O. europaea* var. *sylvestris.*
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The number of seeds from wild plants is similar for stone marten (14.07 seeds/scat) and red fox (16.13 seeds/scat).

The number of dispersed seeds is distributed almost equally in summer (29.0%), autumn (33.5%) and winter (37.3%), while the amount of seeds dispersed during the spring is very low (0.2%). The multivariate ANOVA comparing the number of seeds reflects this differential dispersal along the seasons for *A. ovalis* (*F*=4.909, *p*=0.008), *Celtis australis* L. (*F*=3.326, *p*=0.037), *J. phoenicea* (*F*=4.175, *p*=0.016), *R. alaternus* (*F*=5.035, *p*=0.008), *R. ulmifolius* (*F*=3.121, *p*=0.045) and *O. europaea* (*F*=6.043, *p*=0.003). Stone marten and red fox disperse these species in the same proportion, except for *O. europaea* (*F*=8.907, *p*=0.006), being the fox the main disperser.

The high number of *R. ulmifolius* consumed by red fox is significant (*F*=8.907, *p*=0.006).

Table 3 shows how stone marten disperses mainly seeds of *J. phoenicea*, and also *R. alaternus* and *A. ovalis*. Red fox contributes to the seed dispersal of *J. phoenicea* and *R. alaternus*, but disperses a higher amount of seeds of *Rubus ulmifolius* Schott.

Nevertheless, the high number of *R. ulmifolius*...
seeds found is concentrated only three scats for the red fox and one for the stone marten (Table 3). The same happens with \textit{F. carica} in the case of the stone marten. Red fox seems to feed on it more than stone marten, but the amount of seeds found corresponds approximately to only 1.6 fruits. On the contrary, \textit{J. phoenicea} and \textit{R. alaternus} are frequently consumed by both carnivores, as the number of scats in which their seeds appear and the estimated number of fruits consumed is high. Stone marten shows some preference also for \textit{A. ovalis}. Among domesticated species, stone marten prefers \textit{P. avium}, while red fox feeds regularly on \textit{O. europaea}.

The probability of presence in the core area of the eight plant species considered in the analysis is correlated with the presence of their seeds in stone marten scats, but the results are just marginally significant ($r=0.646$; $p=0.084$). The frequency of presence of \textit{P. avium} is higher in stone marten scats than in the area. The same happens for \textit{O. europaea} in red fox scats in a lower proportion (Table 1). The probability of presence of \textit{F. carica} in the Natural Park is also similar to the probability of presence of its seeds in red fox scats.

Table 2. Significant results for the Kruskal-Wallis test, showing the species with differences in the number of seeds dispersed along the seasons.

<table>
<thead>
<tr>
<th>Plant Species</th>
<th>Stone marten (n)</th>
<th>Red fox (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\chi^2$</td>
<td>$p$</td>
</tr>
<tr>
<td>\textit{A. ovalis}</td>
<td>10.253</td>
<td>0.017*</td>
</tr>
<tr>
<td>\textit{C. australis}</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>\textit{J. phoenicea}</td>
<td>11.291</td>
<td>0.010**</td>
</tr>
<tr>
<td>\textit{P. avium}</td>
<td>6.482</td>
<td>0.090m</td>
</tr>
<tr>
<td>\textit{R. alaternus}</td>
<td>14.619</td>
<td>0.002**</td>
</tr>
</tbody>
</table>

** Significant for $p \leq 0.01$
* Significant for $p \leq 0.05$
= Marginally significant

Figure 4. Average number of seeds per week of each plant species found in the scats of stone marten with the standard deviation for each season. The asterisks indicate the $p$-value ($p \leq 0.05$) of the Mann-Whitney's U test.

Figure 5. Average number of seeds per week of each plant species found in the scats of red fox with the standard deviation for each season. The asterisks indicate the $p$-value ($p \leq 0.05$) of the Mann-Whitney's U test, and the letters show the similarity among the subsets.
When comparing the relative percentage of pulp weight between the two species of *Juniperus* sp., the results show that *J. phoenicea* \((x=78.05\% \pm 2.74, n=14)\) has a higher percentage of pulp in terms of relative weight than *J. oxycedrus* \((x=66.35\% \pm 11.62, n=14)\) with high significance \((F=13.454, p=0.001)\).

Discussion

Among the most dispersed plant species, stone marten exploits mainly *J. phoenicea* and *A. ovalis*. This has been observed in similar habitats (Padial et al. 2002). *R. alaternus* is the only species which stone marten and fox disperse in the same proportion. Many studies give evidence of *R. alaternus* being dispersed mainly by birds (Gulias et al. 2004, Bas et al. 2006) and also by ants (Aronne & Wilcock 1994, Bas & Gómez 2001, Bas et al. 2009). Some avian dispersers feed on *R. alaternus* while they are in their breeding season, when they become more territorial (Bas et al. 2006). This means that seeds remain near parental individuals. Carnivores have larger vital areas and travel larger distances than ants and birds. They could play a part in long distance seed dispersal of this species. However, the role of carnivore mammals in its dispersal has not been studied. The species *C. australis* has a noticeable importance on fox's diet. A study by Traba et al. (2006) has proved that red fox has a relevant role in its dispersal, favouring seed germination and seedling growth.

On the other hand, the consumption of *R. ulmifolius* appears to be less common in both species. The low frequency and the high number of seeds found in the scats suggests that the animal visits the shrub in very few occasions, but feeds on it very thoroughly. This species is as abundant in the area as the two most consumed wild species (Serra & Soler 2011), so this might mean that both carnivores do not show preference for this species in particular.

As stated by Padial et al. (2002), red fox seems to have greater interest for domesticated species. It seems to extend its vital area outside the Natural Park, where domesticated and cultivated species are more abundant. Nevertheless, stone marten shows a remarkable preference for *P. avium*. This species can only be found growing outside the core areas far as we know. This could mean that the animal travels some distance to get to the tree or that there exist some unnoticed wild individuals in the core area. Anyway, stone marten shows a tendency to feed more on plant species which are more present in the core area of the Natural Park.

Most of the plant species considered are shrubs with black or brown fruits after ripening, colours that are not among the preferred by carnivores according to Herrera (1989). In this case, the seven most abundant species in the scats have fruits with these characteristics. The particular case of *J. phoenicea* in our study is remarkable. A similar species of juniper, *J. oxycedrus*, is present in the study area, and both species are also very abundant (Serra & Soler 2011). Nevertheless, evidences in size and shape of the seeds and also the remaining squamiform leaves found did not leave a reason to doubt. Fruits of *J.

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**Table 3.** Total sum of the seeds of each species found in the scats, the number of scats containing these seeds and the correspondent estimated number of fruits for each carnivore.

<table>
<thead>
<tr>
<th></th>
<th>Stone marten</th>
<th></th>
<th></th>
<th>Red fox</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Seeds</td>
<td>Scats</td>
<td>Fruits</td>
<td>Seeds</td>
<td>Scats</td>
<td>Fruits</td>
</tr>
<tr>
<td><em>A. ovalis</em></td>
<td>300</td>
<td>19</td>
<td>75</td>
<td>62</td>
<td>6</td>
<td>16</td>
</tr>
<tr>
<td><em>C. australis</em></td>
<td>4</td>
<td>1</td>
<td>4</td>
<td>33</td>
<td>7</td>
<td>33</td>
</tr>
<tr>
<td><em>J. phoenicea</em></td>
<td>1,414</td>
<td>23</td>
<td>177</td>
<td>588</td>
<td>15</td>
<td>73.5</td>
</tr>
<tr>
<td><em>R. alaternus</em></td>
<td>413</td>
<td>19</td>
<td>138</td>
<td>459</td>
<td>16</td>
<td>153</td>
</tr>
<tr>
<td><em>R. ulmifolius</em></td>
<td>106</td>
<td>1</td>
<td>2.1</td>
<td>1,650</td>
<td>3</td>
<td>33</td>
</tr>
<tr>
<td><strong>Wild species</strong></td>
<td><strong>2,237</strong></td>
<td><strong>63</strong></td>
<td>-</td>
<td><strong>2,792</strong></td>
<td><strong>47</strong></td>
<td>-</td>
</tr>
<tr>
<td><em>O. europaea</em></td>
<td>4</td>
<td>2</td>
<td>4</td>
<td>76</td>
<td>14</td>
<td>76</td>
</tr>
<tr>
<td><em>P. avium</em></td>
<td>21</td>
<td>7</td>
<td>21</td>
<td>3</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><strong>Domesticated species</strong></td>
<td><strong>25</strong></td>
<td><strong>12</strong></td>
<td>-</td>
<td><strong>79</strong></td>
<td><strong>36</strong></td>
<td>-</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>2,262</td>
<td>72</td>
<td>-</td>
<td>2,871</td>
<td>63</td>
<td>-</td>
</tr>
</tbody>
</table>
phoenicea seem to have a higher relative pulp weight than J. oxycedrus ones. It has also been noticed that the pulp of J. phoenicea fruits has a stronger smell compared with J. oxycedrus, although this has not been tested. These facts could have an influence in the preference shown by the red fox and specially the stone marten, which also shares habitat with J. phoenicea. Stone martens can be found living in rocky spots, with cracks and fissures (Blanco 1998, Powell 2001). This species of juniper also grows in places with very little soil and good drainage, as stone walls and areas of stony ground. A study by Delibes (1978) showed that stone marten feeds mostly on J. phoenicea among other wild shrubs in similar forest and rocky environments.

The results show that the role of red fox and stone marten as seed dispersers is important and should be studied with deeper interest and during longer periods to detect clearer patterns and preferences. Concerning seasonality among the plant species, it would be necessary to study how the fruit consumption and fruit phenology of the consumed species adjust to each other in time. This work is part of a wider study currently in progress, in which other determinant factors of endozoochorous seed dispersal by mammals and their applications to restoration ecology are analysed.

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References


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