



Rodents change acorn dispersal behaviour in response to ungulate presence

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Small rodents are prominent seed predators, but they also favour plant recruitment as seed dispersers. The direct interactions of ungulates on plants are more one-sided and negative, as they mainly reduce plant recruitment through predation on seeds and seedlings. The effects of small rodents and ungulates on plant recruitment have been considered and studied as independent episodes within plant regeneration cycles. However, ungulate–rodent interactions and their potential effects on plant regeneration have not been considered so far. A number of studies have recently documented ungulate effects on the abundance, diversity and spatial distribution of small rodents. Here, we hypothesize that ungulates may also affect rodent seed dispersal behaviour. We monitored acorn dispersal by small rodents (*Mus spretus* and *Apodemus sylvaticus*) in oak woodlands with and without exclosures for large ungulates, mainly red deer, *Cervus elaphus*, and wild boar, *Sus scrofa*. The study was carried out in a typical Mediterranean Holm oak, *Quercus ilex*, forest throughout the acorn fall season in 2003 and 2004. We found that, in both years, the proportion of acorns cached and not recovered in the short-term was, on average, lower in the presence (1.4%) than in the absence (19.9%) of ungulates. Acorn dispersal distances were not affected by ungulate presence in either year. However, ungulates had an effect on the spatial distribution of dispersed seeds; rodents apparently avoided shrubs as caching sites in both years. This result was interpreted as a behavioural response to reduce the risk of cache pilferage by conspecifics, which are closely associated with shrubs in presence, but not in absence, of ungulates. Potential effects of different densities of rodents or predators were discarded, as none of them differed between the areas with and without ungulates. The present study found significant interactions between heterospecific seed and seedling consumers that had been considered as independent episodes within tree regeneration cycles. As a result of such interactions, ungulates may have negative indirect effects on oak recruitment by reducing (1) acorn caching frequency, and (2) the proportion of acorns cached under shrubs, key nurse-plants for the establishment of Holm oak seedlings in Mediterranean areas.

Rodents are prominent seed predators, but they also disperse and cache seeds, thus enhancing plant recruitment (Jensen and Nielsen 1986, Vander Wall 1990, Brewer and Rejmanek 1999, Jansen et al. 2002, Roth and Vander Wall 2005). On the other hand, ungulates are known to decrease tree regeneration as they are major predators of seeds and seedlings (Crawley 1997, Ickes et al. 2001, Tsujino and Yumoto 2004). Recent studies have shown that ungulates also decrease the abundance, diversity and body condition of small mammals and can alter their spatial distribution (Keesing 1998, Moser and Witmer 2000, Smit et al.

2001, Muñoz 2005). Nonetheless, it has not been considered whether ungulates could also have an effect on rodent dispersal behaviour and thus on plant recruitment. In fact, ungulate and rodent effects on plants have been studied as independent processes within plant regeneration cycles so far (Pulido and Díaz 2005). In the present study, we hypothesize that ungulates may mediate rodent–plant interactions by altering the patterns of seed dispersal.

Directed dispersal of seeds to sites that fulfil the requirements for seedling establishment (safe sites) has been pointed out as a measure of the effectiveness of

seed dispersing rodents (Vander Wall 1993, Wenny 2001, Hollander and Vander Wall 2004). In several plant species, shrubs can act as safe sites because they may favour germination and seedling establishment by ameliorating stressful physical conditions (Gómez-Aparicio et al. 2005) and providing protection from predators (Callaway 1992, Rousset and Lepart 1999). Hence, the effectiveness of rodents as seed dispersers in shrub-facilitated plants is directly related with the proportion of seeds they cache under shrubs. In the present study, we specifically assess whether seed dispersal to shrubs could be altered by ungulate presence. Recent evidence suggests that the decisions on where to cache seeds are strongly influenced by the probability of cache pilferage by conspecifics (Preston and Jacobs 2005, Dally et al. 2005). Ungulates can influence rodent spatial distribution, increasing the association of rodents with shrubs, since shrubs seem to act as shelter against ungulate direct disturbances as rooting and trampling (Muñoz 2005). This strong association of rodents with shrubs in the presence of ungulates may lead to a higher probability of cache pilferage by conspecific rodents under shrubs, and thus rodents would be expected to cache preferentially outside shrubs when ungulates are present. On the other side, caching seeds outside shrubs may increase cache predation likelihood by ungulates like wild boars (Focardi et al. 2000, Gómez et al. 2003). Thus, rodents may face a dilemma in their caching decisions regarding vegetation structure (den Ouden et al. 2005), and thus, the selection of shrubs as caching sites could be strongly influenced by ungulate presence.

In order to shed light on these issues we used the dispersal of Holm oak, *Quercus ilex*, acorns by rodents as a model. Oaks are a suitable study case, because acorns are often dispersed by rodents (Jensen and Nielsen 1986, Vander Wall 2001, Xiao et al. 2004, den Ouden et al. 2005), and shrubs can facilitate acorn germination and seedling establishment (Callaway 1992, Rousset and Lepart 1999). In the Mediterranean *Q. ilex*, shrubs improve seedling survival by diminishing air temperature, radiation and vapour pressure deficit, thus favouring water balance in seedlings (Gómez-Aparicio et al. 2005). This facilitation increases seedling survival likelihood to the first summer drought, one of the most critical recruitment stages in the dry Mediterranean areas where the Holm oak is common (Gómez-Aparicio et al. 2005, Pulido and Díaz 2005). In fact, lack of shrubs is considered as the main bottleneck for recruitment in this tree (Pulido and Díaz 2005). In the present study, we specifically tested whether ungulates may influence: (1) the proportion of acorns used by rodents, (2) the probability an acorn is dispersed vs consumed by rodents, (3) acorn dispersal distances, and (4) the proportion of acorns cached under vs outside of shrubs.

Material and methods

Study area

The study was conducted at the Cabañeros National Park (central Spain, 39°24'N, 3°35'W) from September to February, 2003–2004, and 2004–2005. The study area is a typical Mediterranean Holm oak, *Quercus ilex*, forest with a 50–60% shrub cover, mainly of *Cistus ladanifer*, *Phillyrea angustifolia* and *Erica arborea*. Ungulates are abundant, as big game hunting was one of the main human uses in this area, which lasted until the declaration of the National Park in 1995. As a result of this past use the densities of large ungulates, principally red deer, *Cervus elaphus*, and wild boar, *Sus scrofa*, are high (0.14 individuals ha⁻¹ for *C. elaphus*; Jiménez 2004). Roe deer, *Capreolus capreolus*, is also present, but in far fewer numbers. Previous trapping has demonstrated that the Algerian mouse, *Mus spretus*, is by far the most abundant rodent at the study area (more than 85% of all rodents captured in 3600 traps night⁻¹), although some wood mice, *Apodemus sylvaticus*, were trapped as well (less than 15% of all rodents captured in 3600 traps night⁻¹; Muñoz 2005). Acorns constitute the bulk of rodent diet during acorn fall in autumn (September–January) and both rodent species are prominent acorn dispersers (den Ouden et al. 2005, Pulido and Díaz 2005, Muñoz 2005).

Experimental design

We selected a sample of 22 Holm oaks to monitor acorn predation and dispersal by rodents. Half of the selected trees (11) were located in a forest where ungulates had been excluded since 1995. This area has an extension of 5–6 ha and the enclosure were made with a 2 m tall fence with a mesh width of 32 × 16 cm. This fence excludes ungulates, but allows the passage of the predators of small rodents present at the National Park, mainly red foxes, *Vulpes vulpes*, genets, *Genetta genetta*, stone martens, *Martes foina*, and wild cats, *Felis sylvestrus* (Díaz et al. 2004). This fact is important to be able to attribute any effect of the enclosure on rodents to the absence of ungulates without any confounding effect of a parallel decrease of predation pressure. In fact, we performed counts of predator scats from 2001 to date in 10 × 30 m transects that were located in the areas with and without ungulates (three transects per ungulate treatment). Transects were permanently marked and visited in autumn (November), when scats were searched intensively and counted. At the study site, 95% of scats belonged to red foxes, the largest terrestrial predator of the National Park. Its scats are easily identifiable, due to their size and shape and also because

they often contain remains of arthropods and seeds of fleshy fruits, which are a common food source at the study site. The remaining 5% were stone marten scats, easy to recognize because of their characteristic U-shape. The density of scats recorded has been quite the same and very low in all censuses, being the densities similar in presence (1.1 ± 0.18 scats ha^{-1}) or absence (1.0 ± 0.29 scats ha^{-1}) of ungulates ($F_{1,18} = 0.082$, $p = 0.78$). This low number of scats also confirms the extremely low densities of terrestrial predators at our study site (Díaz et al. 2004). Focal trees were distributed along both sides of the fence and at least 35 m from the fence and from the nearest study tree. This design ensures independence between the rodent foraging behaviour recorded at each tree, as that distance is much larger than the home ranges of radio-tracked rodents at the study area (home ranges estimated ranged from 90 to 130 m^2 , with maximum linear displacements of 25 m, unpubl.). Thus, each tree can be considered as an independent replicate in the analyses of acorn dispersal behaviour.

At each study tree, we monitored acorn predation and dispersal by placing 2–4 feeding plots (50 × 50 cm) on the ground below the canopy. The number of feeding plots per tree was proportional to the canopy surface. Feeding plots were protected from other post-dispersal acorn consumers (i.e. birds and ungulates) using 50 × 50 × 20 cm wire cages with a mesh size of 5 × 5 cm, which only allowed the entrance of rodents. At each feeding plot, we placed three sound acorns from the oak above. We discarded acorns infested by the chestnut weevil, *Curculio elephas*, the most prominent predispersal predator of Holm oak acorns (Bonal et al. 2007), as weevil infestation can influence rodent foraging decisions (Steele et al. 1996, Muñoz 2005). Infested acorns are easily identifiable due to the small puncture made by females to oviposit (Bonal and Muñoz 2007, Bonal et al. 2007). Sound acorns were marked with 50 cm of fluorescent fishing line with 5 cm of fluorescent pink flagging tape at one extreme to facilitate acorn location after removal. This methodology is not considered to influence rodent foraging behaviour (Forget and Wenny 2005). Furthermore, any differences in behaviour between the areas with and without ungulates are unlikely to be due to the lines attached to acorns given that acorns in both ungulate treatments were marked in this way. Using this methodology, we were able to locate more than 90% of the removed acorns (for similar procedure see Forget 1990, Jansen et al. 2002). Acorns were manipulated using fresh gloves to avoid effects of human handling on rodent foraging decisions (Wenny 2002).

In 2003 and 2004 we checked all marked acorns every 10 days during the whole acorn drop season, which lasts from September to January. At each check, all marked acorns were classified as used or not by

rodents. Those used were in turn classified as (1) eaten at the feeding plots, (2) dispersed and eaten within the time elapsed between two consecutive censuses (i.e. 10 days), and (3) dispersed and not eaten within two consecutive censuses. At each revision we searched intensively for every removed acorn, recording the dispersal distance and whether they were cached under shrubs or not. Used acorns were replaced with freshly marked acorns at the feeding plots.

Rodents were live-trapped in November 2003 and 2004 at the study area to test for potential differences in rodent abundance between the areas with and without ungulates. We established 16 paired trapping stations, placed on both sides of the fence. Each trapping station consisted of 10 Sherman live-traps laid out in two lines parallel to the fence, with a distance between traps of 10 m, and at least 50 m to the fence. Each session consisted of two sets of 3 trap-nights (each session produced 240 trap-nights), one just before and the other after the new moon in order to avoid any confounding effect of moonlight on rodent activity and trappability (Díaz 1992).

Data analyses

We used ANOVA to test for differences in the acorn dispersal behaviour of rodents in the areas with and without ungulates. We included the year as categorical factor to test for any potential interannual effects on the patterns observed. We also studied the spatial distribution of the acorns dispersed and assessed whether they were preferentially carried under shrubs or not. This was done using the Jacobs selection index (Jacobs 1974), which estimates to what extent shrubs are selected taking into account shrub availability. An acorn was considered to be dispersed under shrubs when it was cached below the vertical cover of shrubs. The Jacobs selection index was calculated for the acorns dispersed at each focal tree. Shrub abundance was estimated visually around each focal tree over an imaginary circle that comprised all the locations of the acorns dispersed by rodents. In most cases, this circle covered an area of approximately 100 m^2 , which coincides with the home ranges we measured using radio tracking for *Mus spretus* at the study area. Both authors estimated independently the shrub cover in all focal trees, and the measures were highly repeatable ($r > 0.98$; $p \ll 0.001$). Jacobs index value ranges from -1 (total avoidance of shrubs) to 1 (strongest preference for shrubs). A value of 0 would indicate random selection (i.e. shrubs selected according to their availability). We tested whether the Jacobs selection index differed from 0 in the focal trees with and without ungulates, and also analysed the differences in the index values between both groups.

Results

The Algerian mouse was the most common rodent species captured at the study area in 2003 and 2004, representing 95% of all rodents trapped in both years; wood mouse made up all remaining captures. Overall, rodent abundance was significantly higher in 2003 (1.68 ± 0.32) than in 2004 (0.5 ± 0.18 rodents/30 trap-nights; $F_{1,28} = 9.75$, $p = 0.004$), but did not differ between the areas with (0.96 ± 0.29) and without ungulates (1.25 ± 0.31 rodents/30 trap-nights) in either year (exclusion effects: $F_{1,28} = 0.67$, $p = 0.42$; exclusion \times year interaction: $F_{1,28} = 0.24$, $p = 0.63$).

In 2003 we marked and monitored a total of 635 acorns. Acorn drop started in early October (first observed was on 6 October) and lasted until early January (last check 3 January). In 2004 we monitored 1223 acorns from 23 September to 4 February, when acorn drop ceased. The proportion of acorns used by rodents was higher in 2003 (43%) than in 2004 (26%) ($F_{1,40} = 7.07$, $p = 0.01$). This was mainly because the proportion of acorns used was extremely low in 2004 where ungulates were absent (year \times ungulate interaction, $F_{1,40} = 5.52$, $p = 0.023$; Fig. 1)

Each year, approximately one half of the acorns used by rodents were eaten at the feeding plots, and the rest were dispersed (Fig. 2). Most dispersed acorns were cached singly, usually buried at a depth of 1.5–2 cm under the ground or under litter, and a significant proportion of caches were recovered or predated by rodents within the 10 days between consecutive

censuses (Fig. 2). Recovery and predation of cached acorns was easily detected thanks to the small holes excavated by rodents at the cache site and the presence of the fishing line with the pink flagging tape. The proportion of caches not recovered within 10 days averaged 9.4% of all used acorns (Fig. 2), with no differences between years (interaction with year $F_{1,24} = 0.66$, $p = 0.42$). However, recovery and predation on cached acorns was faster in presence than in absence of ungulates; indeed, only 1.4% of cached acorns from the area with ungulates were not predated by rodents in the 10 day-period vs 19.9% in the excluded areas (ungulate effect $F_{1,24} = 5.39$, $p = 0.02$). This result did not change between years (interaction ungulates \times year $F_{1,24} = 1.57$, $p = 0.22$; Fig. 2). Wild boar predation affected just 7% of the caches, and was easily identified because the soil was heavily trampled and rooted.

Dispersal distances were significantly larger in 2003 (mean \pm SE = 198.5 ± 17.9 cm, $n = 142$) than in 2004 (mean \pm SE = 137.2 ± 22.6 cm, $n = 161$; $F_{1,32} = 9.32$, $p = 0.004$), but did not differ between ungulate treatments (ungulates $F_{1,32} = 0.04$, $p = 0.83$; ungulate \times year $F_{1,32} = 0.24$, $p = 0.62$). By contrast, ungulates had a significant effect on the distribution of dispersed seeds in relation to shrub cover. The values of the Jacobs selection index testing for rodent preferences to cache the acorns under shrubs did not differ significantly from 0 in absence of ungulates ($t_{18} = -0.45$, $p = 0.65$; Fig. 3). Thus, acorns were moved to shrubs according to shrub availability. However, where ungulates were present, the Jacobs

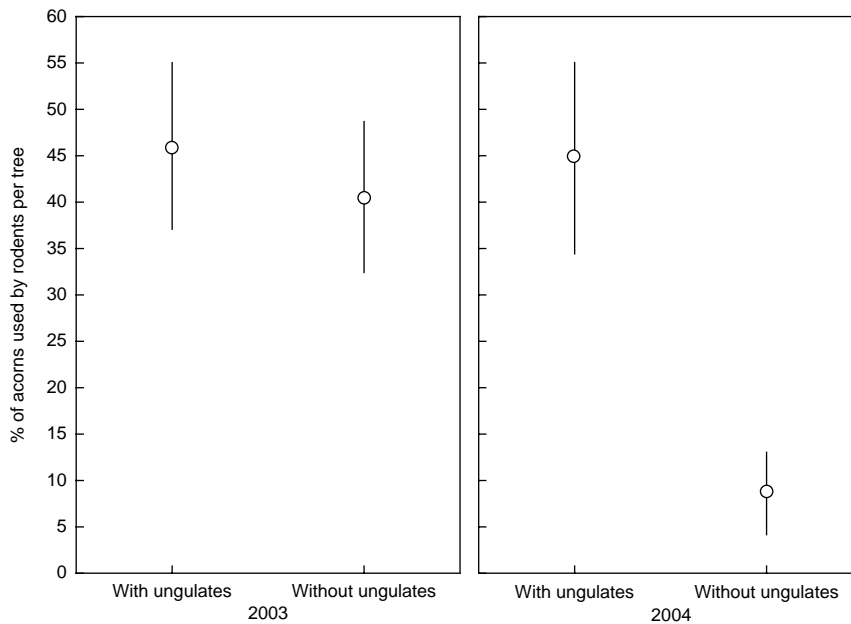


Fig. 1. Proportion of acorns used by rodents (mean \pm SE) in the areas with and without ungulates during the acorn fall season of 2003 and 2004.

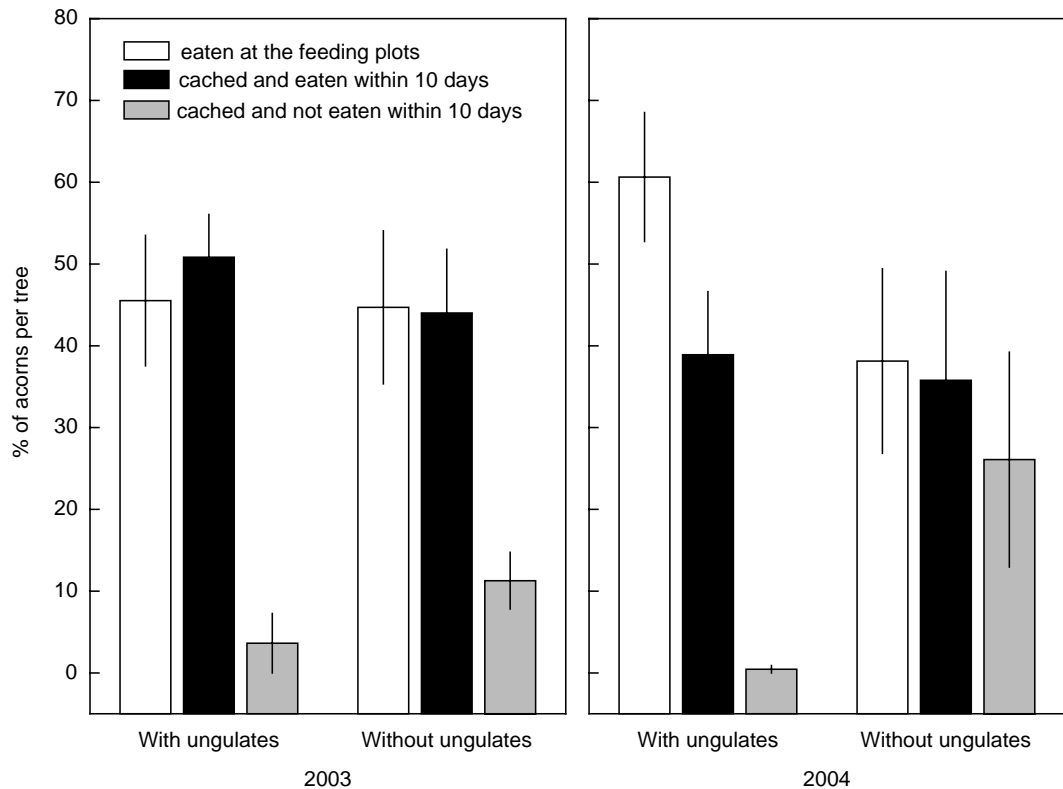


Fig. 2. Proportion of used acorns (mean \pm SE) that were (1) eaten at the feeding plots, (2) cached and eaten within 10 days and, (3) cached and not eaten within 10 days by rodents in the areas with and without unguulates during the acorn fall season of 2003 and 2004.

selection index differed significantly from 0 ($t_{18} = -4.77$, $p < 0.001$) and was negative, showing that shrubs were avoided by rodents as microhabitats for caching acorns (Fig. 3). Thus, the selection index was significantly different between unguulate treatments (ANOVA: unguulate effects $F_{1,33} = 4.83$, $p = 0.035$), and these differences held between years (year \times unguulates interaction, $F_{1,33} = 0.27$, $p = 0.44$; Fig. 3).

Discussion

This study demonstrates that wild unguulates have significant effects on the seed dispersal behaviour of small rodents. First, the proportion of acorns used by rodents was similar across years and treatments, except in the unguulate-excluded area in 2004, which had significantly lower acorn use by rodents. This lower acorn use in absence of unguulates may be also related to the overall lower abundance of rodents documented in 2004 (from 2003 to 2004 rodent abundance decreased in a 71%). The low abundance of rodents along with the absence of acorn predation by unguulates resulted

in a high acorn availability and thus in lower use of experimental acorns in the excluded area. However, as unguulates also consume acorns, acorn availability decreases when they are present, and thus the use of experimental acorns by rodents increases. These differences were probably precluded in 2003 due to the general higher rodent abundance documented and the significantly lower acorn crops compared to 2004 (in 2004 focal trees increased their production in a 26% on average, 1595 ± 360 acorns tree^{-1} as compared to 1179 ± 293 acorns tree^{-1} in 2003, Bonal and Muñoz 2007). Both smaller crops and higher rodent abundance may have resulted in a lower acorn availability in both unguulate excluded and unexcluded areas in 2003 and thus in a higher use of the experimental acorns everywhere, provoking these between-year differences in the effects of unguulates on the use of experimental acorns by rodents.

We found that the proportion of acorns cached and recovered/predated by rodents within 10 days (i.e. between two consecutive censuses) was higher in presence than in absence of unguulates in 2003 and 2004. Some caches in our study area were predated by wild boars, as has also been documented by Focardi

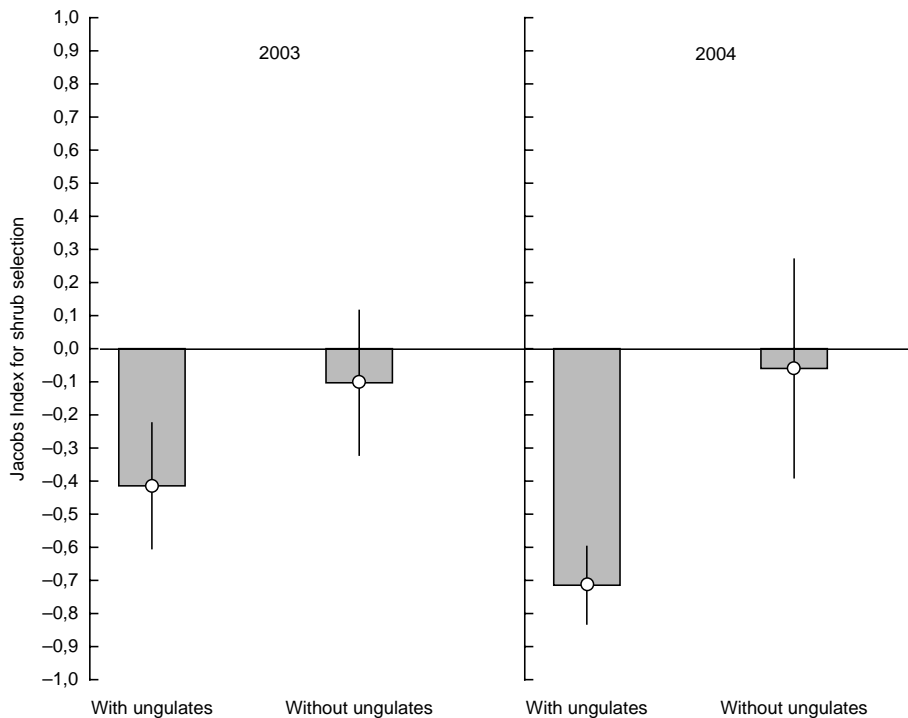


Fig. 3. Values of the Jacobs selection index (mean \pm SE) testing for rodent preferences to carry the acorns under shrubs, in the areas with and without ungulates during the acorn fall season of 2003 and 2004. The index ranges from -1 (total avoidance of shrubs) to 1 (strongest preference for shrubs). A value of 0 would indicate no preferences for shrubs (Jacobs 1974).

et al. (2000). Thus, the risk of cache predation by wild boars could explain why rodents recovered the caches faster when ungulates were present. In addition, reductions of acorn availability due to ungulate consumption could also increase the likelihood of cache robbery by conspecifics, what might also lead the caching rodents to a sooner recovery of the acorns.

Dispersal distances were longer in 2003 than in 2004, but did not differ between the areas with and without ungulates in either year. These between-year differences suggest that dispersal distances are negatively related to acorn availability, as 2003 was a year with a higher rodent abundance and lower acorn crop, and 2004 had a lower rodent abundance and higher acorn crop. This result agrees with other studies showing that seed dispersal distances by rodents are shorter in large crop years than in lean years (Jansen et al. 2004). In addition, the lack of an effect of ungulates on dispersal distance suggests that the reduction of acorn availability by ungulates is negligible compared with the strong between-year differences in rodent and acorn abundance.

Our results show that ungulates had significant effects on the spatial distribution of dispersed acorns in relation to shrubs. In both study years, rodents cached the acorns under shrubs according to shrub availability in absence of ungulates, but shrubs were

actively avoided for acorn caching where ungulates were present. This finding is very relevant, as the influence of the microhabitat on rodent caching decisions had not received much attention so far. Most studies have been focused on seed predation instead, showing that it is more frequent under shrubs probably because of the lower predation risk for the rodents under shrub cover (Manson and Stiles 1998, Russell and Schupp 1998, Mohr et al. 2003, Ji-Qi and Zhi-Bin 2004). Our results cannot be explained by differential predation risk, as our scat counts suggest that predator densities are similar in the areas with and without ungulates. Instead, we suggest that the avoidance of shrubs for acorn caching in presence of ungulates could be a mechanism to reduce the risk of cache pilferage by conspecifics. We had previously found that, although ungulates do not reduce the shrub cover, they alter the distribution and activity of rodents which are closely associated with shrubs when ungulates are present (Muñoz 2005). This is probably because rodents use the shrubs as refuge against ungulate physical disturbances like soil compaction or rooting (Muñoz 2005). So, the pilferage of acorns cached under shrubs could increase in presence of ungulates due to the higher occurrence of rodents under shrubs. The influence of cache pilferage by conspecifics on seed caching decisions has been reported in other species recently. For example, Merriam's

kangaroo rat, *Dipodomys merriami*, moves seeds to less preferred sites when the risk of pilferage by conspecifics is high (Preston and Jacobs 2005). Similarly, western scrub-jays, *Aphelocoma californica*, prefer to cache food items in distant sites when watched by another conspecific jay to reduce visual information available to the potential thief (Dally et al. 2005). Our results suggest that in the areas with ungulates rodents might avoid shrubs for caching to prevent cache pilferage by conspecifics, which could be, on the other side, also more prone to search and rob caches due to the reduction of acorn availability by ungulate consumption. This is supported by the faster cache recovery that we found in presence of ungulates. Nevertheless, it would be necessary to have direct evidence on whether cache pilferage by rodents under shrubs is higher in presence than in absence of ungulates to prove explicitly this hypothesis. Moreover, it would also be interesting to test whether caching acorns outside shrubs could, on the other side, increase the risk of cache predation by wild boars.

Our study examined two critical groups of organisms that shape plant regeneration cycles, ungulates and rodents. The former often have a strong negative effect on plant recruitment as seed/seedling predators (Ickes et al. 2001, Gómez et al. 2003, Tsujino and Yumoto 2004). In fact, they account for most postdispersal predation of Holm oak acorns on the Iberian peninsula (Pulido and Díaz 2005). Rodents, besides being seed predators, also disperse and cache seeds, and may enhance oak recruitment (Jensen and Nielsen 1986, Xiao et al. 2004, Pulido and Díaz 2005, Roth and Vander Wall 2005). Here we show that ungulate and rodent interactions with oaks are not entirely independent as they were previously considered (Pulido and Díaz 2005), because ungulates altered rodent–oak interactions. Ungulates increased cache predation by rodents, potentially reducing the probability of effective dispersal (i.e. preserved for longer periods in the caches). Ungulates also modified the spatial distribution of dispersed acorns by increasing the proportion of seeds dispersed away from shrubs. Shrubs act as nurse plants by ameliorating stressful physical conditions in hot Mediterranean areas and are a key microhabitat that enhances Holm oak seedling survival (Gómez-Aparicio et al. 2005, Pulido and Díaz 2005). Thus, these changes in seed dispersal patterns as a response to ungulate presence could have important consequences on oak recruitment, although they have to be quantified explicitly with further studies.

Our results point to the importance of taking into account the interactions between heterospecific seed and seedling consumers, rather than considering that they have an independent role within plant regeneration cycles (Schupp 1995, Hulme 1996, Pulido and Díaz 2005). Nonetheless, our results should be taken with

caution due to some methodological limitations, as we performed the study in a forest in which there is a single large area free of ungulates. This scenario let us test the effects of ungulates on seed dispersal behaviour of small rodents, but replicated studies carried out in other habitat types, and with different ungulate densities, will help to increase the strength of our results. These studies will also contribute to increase our knowledge on similar or different indirect ecological interactions, which in general have been poorly quantified (Crawley and Long 1995, DeMattia et al. 2004, Bonal and Muñoz 2007) but that are inherent to the complexity of ecosystem functioning.

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