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ORIGINAL ARTICLE

Risk for the natural regeneration of *Quercus* species due to the expansion of rodent species (*Microtus arvalis*)

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Abstract

The role played by rodents in the colonization of acorn-producing plant species has been interpreted in different ways along time. It has gone from a predation relationship, in which rodents destroy seeds by devouring them, to a mutualistic one, in which they leave part of their caches or, more recently consume part of the cotyledons but leave the embryo intact. We studied how three rodent species, *Apodemus sylvaticus* (wood mouse), *Mus spretus* (Algerian mouse), and *Microtus arvalis* (common vole) treat the acorns they consume. The wood mouse and the Algerian mouse have consumed acorns for a long time and participate in this mutualistic relationship by preserving the embryo. The common vole eats acorns for the first time, as it is not a part of its habitual diet. We observed that this rodent species devours the embryo, as opposed to the other two rodent species that usually eat acorns and modifies its behavior over time, suggesting that its way of eating the acorns is not genetically fixed. The common vole has only recently started to enter the distribution areas of *Quercus* species. Its population density is high during certain periods, reaching plague levels in crops. When its usual food source runs out during these periods, it has to find others which probably include acorns. This rodent species eliminates the embryo during consumption and can, therefore, become a serious problem for acorn-producing species by limiting their colonization process. The three rodent species under study showed the same preference for the *Quercus* species provided, rejecting acorns of *Q. suber* and preferring those of *Q. ilex* subsp. *ballota*.

Significance statement

Microtus arvalis (common vole) is considered as an expansive crop pest species in certain parts of Europe, and in comparison with *Apodemus sylvaticus* (wood mouse) and *Mus spretus* (Algerian mouse), it does not have co-evolutionary history with *Quercus* species. Thus, the common vole is suggested to lack a mutualistic relationship with *Quercus* species where trees benefit from seed-dispersing rodents who then use parts of acorns as a food source. Using laboratory breeding, we showed that two habitual acorn consumers rodent species (wood mouse and Algerian mouse) tend to preserve the acorn embryo, while the expansive common vole that does not include acorns in its diet tend to eat the embryo. We concluded that the feeding behavior of the two habitual acorn consumer benefit the mutualistic relation with *Quercus*, probably due to the results of natural selection, whereas the expansive species not accustomed to eating acorns would impose a high risk to the natural regeneration of *Quercus* species.

Keywords Rodents · Acorns · Partial consumption · Embryo damage · Natural regeneration

Introduction

Previous studies have shown that rodents participate in the colonization process of acorn-producing species (Muñoz and Bonal 2008a, 2011; Morán-López et al. 2015) by dispersing and storing their seeds (Vander Wall 2010; Lichti et al. 2017). However, their contribution was interpreted in different ways over time. It was originally considered to be a predation relationship (Pérez-Ramos and Marañón 2008; Pérez-Ramos et al. 2013). Dispersal studies consider only two possible seed fates, either predation or escape intact, and they usually assume

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partial consumption of seeds as equivalent to seed death (Perea et al. 2011b). These studies asserted that the decrease in the capacity of dispersion was the result of predation (Pérez-Ramos et al. 2013).

Later, it was verified that many acorns were not devoured immediately but buried in caches that were perhaps forgotten, enabling them to germinate and sprout. This would be the positive contribution of the rodents in their mutualistic relationship with the plant (Vander Wall 2001; Beck and Vander Wall 2010; Xiao and Krebs 2015). Vander Wall (2010) states that some plant species manipulate animal behavior during the dispersal process by producing hard coats and synthesizing high concentrations of tannin to increase the handling effort and reduce immediate ingestion, thus making it necessary for the rodents to store the acorns temporarily. Yang and Yi (2012) and Yi et al. (2015) argue that plants carry out this manipulation through the size of the acorn (Muñoz and Bonal 2008a; Perea et al. 2014), providing the cotyledons with more resources than the acorn requires for germination (Perea et al. 2014) in order to attract rodents. This is the effect of predator satiation according to Yang and Yi (2012) and Peguero et al. (2014). Since then, more attention was been paid to rodent behavior during acorn placement in caches (Perea et al. 2016). In particular, because part of these caches might be forgotten and the acorns buried in them can germinate, the direction of the dispersion process does not depend on manipulation by the plant but rather on rodent behavior.

At the beginning of this decade, Perea et al. (2011b) and Yang and Yi (2012) discovered that some rodent species (*Apodemus sylvaticus* and *Eutamias sibiricus*) partially consume acorns. Although working in ecosystems located at a great distance from each other, both research groups verified that rodent species start consuming the acorn from the basal end thus avoiding damage to the embryo, which is located at the opposite end (Hou et al. 2010; Perea et al. 2011b; Yi et al. 2015). They also found that partially eaten acorns with an intact embryo maintain their capacity to germinate even when a small portion of cotyledons has been consumed (Perea et al. 2011b; Yi et al. 2015). What is more, these partially devoured acorns germinate more rapidly than whole ones (Yang and Yi 2012). This discovery is highly significant in the plant colonization process, as some of the acorns that seemed to have been destroyed by predation could germinate and establish themselves as seedlings. Predation represents a reduction in resources because part of the cotyledons is consumed but, nonetheless, the germination process continues.

Research into acorn dispersal by rodents should now focus on their behavior during the consumption stage. Some rodent species partially consume acorns (Yi et al. 2013), probably due to satiation caused by the relationship between rodent body size and acorn size (Bonal et al. 2007; Muñoz and Bonal 2008a; Perea et al. 2012). The amount of acorns eaten during partial consumption is not higher than 60–66%; these are the critical values suggested by Perea et al. (2011b) and Yi et al. (2015) above which germination ability of acorns is damaged. Of greater importance is the fact that rodents keep the embryo intact (Steele et al. 1993; Perea et al. 2011b; Yang and Yi 2012; Yi et al. 2015). According to Steele et al. (1993), the plant is responsible for this behavior because it synthesizes high concentrations of tannins around the embryo as the acorn ripens. These recalcitrant substances discourage rodents from ingesting this essential part of the acorn (Xiao et al. 2008, 2009; Zhang et al. 2013).

In this study, we compare the behavior of three rodent species during acorn consumption. Two of them are habitual acorn consumers, *Apodemus sylvaticus* Linnaeus 1758 (wood mouse) and *Mus spretus* Lataste 1883 (Algerian mouse) (Perea et al. 2011a; Muñoz et al. 2012; Del Arco and Carretero 2013), which have long occupied the central plateau of the Iberian Peninsula, where several species of acorn-producing *Quercus* can be found. The third species, *Microtus arvalis* Pallas 1778 (common vole), has gradually migrated down from the mountains towards this central plateau over the last 50 years as the expansion of irrigated crops has attracted them (Paz et al. 2012; Luque-Larena et al. 2013). The diet of this latter species includes fresh green plants but not acorns, since acorns were never available to them. At present, its distribution is associated with crops, but it is possible that for the lack of resources, it may in the future move to forested areas where it could use acorns as a new food source.

We expect to find differences in the embryo-preserving behavior between this non-habitual acorn consumer rodent species in the area (common vole) and the other two rodents (wood mouse and Algerian mouse) that have maintained a mutualistic relationship with acorn-producing plants. We hypothesize that common vole has not yet acquired this mutualistic relationship due to lack of time. If the presence of tannins around the embryo deters consumption as proposed by Steele et al. (1993), the three rodent species would display the same behavior by preserving it. If not, the behavior of the two species that preserve the embryo would be considered genetically fixed because of their long-standing habit of consuming this food (Sundaram et al. 2015).

The new species in the area may represent a very limiting factor for acorn-producing plants as it could halt their colonization process if it is found to devour the embryo during consumption. This constitutes the main risk of these rodent species occupying the distribution area of *Quercus* species.

Material and methods

Study system

During the autumn of 2015, one male and three females of three different rodent species (wood mouse, Algerian mouse, and common vole) were captured in the Cerrato area near

Palencia, Spain (41° 54′10.51″ N, 4°24′35.00″ W). The wood mouse is a rodent species that has inhabited the Iberian Peninsula since ancient times. Acorns of various *Quercus* species, abundant in the area where it lives, are among its food sources. The Algerian mouse is a rodent species of North African origin but which has also been present in parts of the Iberian Peninsula for a long time. It lives practically in the same habitat as the wood mouse except in the Northern Mountains. It also uses acorns as food source. The common vole is a rodent species that is abundant in central Europe. In the Iberian Peninsula, its distribution has been confined until recently to the Northern Mountains where it feeds on fresh food such as soft green herbaceous plants. Due to the increase in the surface area of irrigated crops, the common vole has expanded to the central Iberian Peninsula, where it presents periods of overpopulation and is considered a recurrent crop pest (Paz et al. 2012; Luque-Larena et al. 2013). This species does not have coevolutionary history with the *Quercus* species because its distribution area is linked to crops and, therefore, acorns have not been its food source.

Also, during the autumn of 2015, acorns of the following *Quercus* species were collected: *Quercus ilex* subsp. *ballota* (Desf.) Samp. (holm oak), *Q. faginea* Lam. (Portuguese oak), *Q. pyrenaica* Willd. (Pyreneen oak), *Q. petraea* (Matt.) Liebl. (sessile oak), and *Q. suber* L. (cork oak). Some acorns of each species were measured and weighed (Table 1) and analyzed for nutrient content (Table 2).

Experimental procedures and design

The specimens of the three rodent species captured were placed in terrariums for reproduction (one male and three females). In order to eliminate any previous acorn consumption experience, nine specimens from the descendants of each rodent species were selected for the experiment (Table 3). The nine individuals of each rodent species were placed in isolated terrariums with a layer of soil that originated from their capture area. The soil layer was 8 cm thick, which allowed them to make burrows. We provided them with water and Harlan food Global Diet 2018 until the beginning of the experiment. The terrarium windows were exposed to natural light only so as to alter their circadian cycle. Rodents were fed only with acorns and an abundant supply of water during the 25 days of the experiment, and their behavior was studied with Bushnell (CAMHDMAX) cameras, which allowed researches to check that the wood and the Algerian mouse have nocturnal activity whereas the common vole has daytime activity.

Every day, each specimen had six acorns of one of the five *Quercus* species used. Six is the maximum number of acorns consumed in 1 day by the most voracious species of the three (common vole), with the most consumed acorn species (*Q. ilex* subsp. *ballota*, hereafter *Q. ilex*) serving as a baseline. Acorns of a different *Quercus* species were offered daily following a revolving order that was repeated cyclically every 5 days. The order was as follows: Qp, Qi, Qpy, Qf, Qs (abbreviations are defined in Table 1).

Acorns are a very nutritious fruit with a large amount of nutrients in the cotyledons, so they are highly appreciated by herbivores of varying sizes. The rodents used in this experiment did not go hungry at any time. Specimens were weighed periodically over the 25 days of the experiment. The variations, both in gain and weight loss, oscillated between 0 and 14% of their initial weights, which did not imply risks to their health.

At the end of the experiment, each specimen consumed 150 acorns, 30 from each of the five *Quercus* species. Taking into account nine specimens per rodent species and three rodent species, the total number of acorns managed during the experiment was 4050. Each acorn was identified with a plastic label. The way in which rodents handled acorns was analyzed: the place where partial consumption started (basal or apical), embryo presence or absence, acorns completely eaten or intact. Acorns were classified into four categories according to the different forms of consumption: intact (I: acorns were not eaten at all), totally eaten acorns (T), basal (B: partially eaten acorns by the basal end on the opposite side to the embryo), and apical (A: partially eaten acorns by the apical end where the embryo is).

Two of the three selected rodent species (wood mouse and Algerian mouse) consume acorns habitually. The third one (common vole) does not include them in its diet. These species were forced to consume them, since it did not have any other source of food. However, common vole accepted well this food source since ingesting more acorns than the other species.

Table 1 Dimensions of acorns from different *Quercus* species (mean ± SE) selected for study. Different letters indicate significance differences between *Quercus* species (Bonferroni test, $p < 0.05$) after significant one-way ANOVAs (weight: $F_{(4,\ 184)} = 78.88$, $p < 0.001$; length: $F_{(4,\ 184)} = 76.91$, $p < 0.001$; width: $F_{(4,\ 184)} = 47.72$, $p < 0.001$)

		Number	Weight (g)	Length (mm)	Width (mm)
Q. petraea	(Qp)	37	4.16 ± 0.09ab	24.39 ± 0.27a	15.06 ± 0.18a
Q. ilex subsp. *ballota*	(Qi)	48	4.54 ± 0.10a	30.30 ± 0.27b	14.86 ± 0.19a
Q. pyrenaica	(Qpy)	48	4.04 ± 0.10b	26.89 ± 0.25c	14.19 ± 0.21a
Q. faginea	(Qf)	44	2.97 ± 0.07c	25.04 ± 0.30a	12.31 ± 0.17b
Q. suber	(Qs)	12	6.68 ± 0.30d	31.48 ± 0.92b	17.24 ± 0.21c

Table 2 Composition of acorns from different *Quercus* species (mean ± SE). Different letters indicate significance differences between *Quercus* species (Bonferroni test, $p < 0.05$) after significant one-way ANOVAs (lignin: $F_{(4,\ 12)} = 21.28$, $p < 0.001$; protein: $F_{(4,\ 12)} = 57.31$, $p < 0.001$; fat: $F_{(4,\ 12)} = 16.29$, $p < 0.001$; sugar: $F_{(4,\ 12)} = 6.88$, $p = 0.004$)

	n	Dry matter (%)			
		Lignin	Protein	Fat	Sugar
Q. petraea	3	0.57 ± 0.02ac	0.46 ± 0.05a	3.86 ± 0.41a	11.50 ± 0.30a
Q. ilex subsp. *ballota*	5	0.24 ± 0.02b	6.32 ± 0.22bc	8.53 ± 0.66b	13.17 ± 0.30a
Q. pyrenaica	3	0.17 ± 0.02b	4.92 ± 0.11b	5.46 ± 0.11a	11.14 ± 0.57a
Q. faginea	3	0.32 ± 0.07bc	4.95 ± 0.19b	4.77 ± 0.22a	16.59 ± 0.80b
Q. suber	3	0.82 ± 0.11c	7.26 ± 0.72c	4.34 ± 0.27a	12.77 ± 1.64a

It was not possible to record data blindly because our study involved focal animals in the laboratory.

Data analyses

The effects of rodent species (wood mouse, Algerian mouse, and common vole), day (5 levels), *Quercus* species (Qp, Qi, Qpy, Qf, Qs), category of acorn consumption (B, A, T, I), and their interactions on the number of acorns eaten per specimen were analyzed using linear mixed models (LMMs) with the restricted maximum likelihood method (REML). The specimens were treated as the random factor and the day as the repeated factor. Finally, working over the model matrix, contrasts were carried out to test differences between fixed factor levels (Pinheiro and Bates 2000). Consequently, the Bonferroni correction was used to adjust for the significance level for each *t* test (Sokal and Rohlf 1995). Statistical computations were implemented in the R software environment (version 2.15.3; R Core Team 2013), using the nlme package for LMM (Pinheiro et al. 2013).

Data availability

The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Table 3 Characteristics of rodent specimes (mean ± SE, $n = 9$) selected for study. Different letters indicate significance differences between rodent species (Tukey test, $p < 0.05$) after significant one-way ANOVA ($F_{(2,\ 24)} = 320.19$, $p < 0.001$)

	Weight (g)	Age (weeks)	Sex ratio (males-females)
Algerian mouse	12.04 ± 0.25a	4–5	5–4
Wood mouse	20.37 ± 0.57b	4–4	5–4
Common vole	32.34 ± 0.68c	4–5	6–3

Results

The LMM analysis showed a highly significant interaction between “category of consumption,” “*Quercus* species,” and “rodent species” (Table 4), suggesting that different rodent species handle acorns of different *Quercus* species in a different way (Fig. 1). In particular, the wood mouse consumes most of the acorns of *Q. petraea*, *Q. ilex*, and *Q. pyrenaica* by the basal end, whereas leaves intact most of the acorns of *Q. faginea* and *Q. suber* but, if consumed, prefers the basal end (Fig. 1a). The Algerian mouse leaves intact most of the acorns of *Q. petraea*, *Q. faginea*, and *Q. suber* but, if consumed, prefers the basal end. In addition, the Algerian mouse consumes most of the acorns of *Q. pyrenaica* and *Q. ilex* by the basal end (Fig. 1b). However, the common vole consumes

Table 4 The summary results of linear mixed models testing the effects of *Quercus* species, rodent species, category of consumption, day, and their interaction on the number of acorns consumed per individual

	df	*F*
Intercept	1, 2280	11,568.164***
Category of consumption	3, 2280	511.863***
Quercus sp.	3, 120	0.017
Rodent sp.	2, 120	0.02
Time	4, 2280	0.015
Consumption**Quercus*	12, 2280	170.573***
Consumption*Rodent	6, 2280	671.959***
*Quercus**Rodent	8, 120	0.013
Consumption*Time	12, 2280	3.126***
*Quercus**Time	16, 2280	0.009
Rodent*Time	8, 2280	0.019
Consumption**Quercus**Rodent	24, 2280	47.051***
Consumption**Quercus**Time	48, 2280	1.23
Consumption*Rodent*Time	24, 2280	2.153***
*Quercus**Rodent*Time	32, 2280	0.022
Consumption**Quercus**Rodent*Time	96, 2280	0.882

The *F* values of the fixed factors and their significance (***$p < 0.001$) are presented

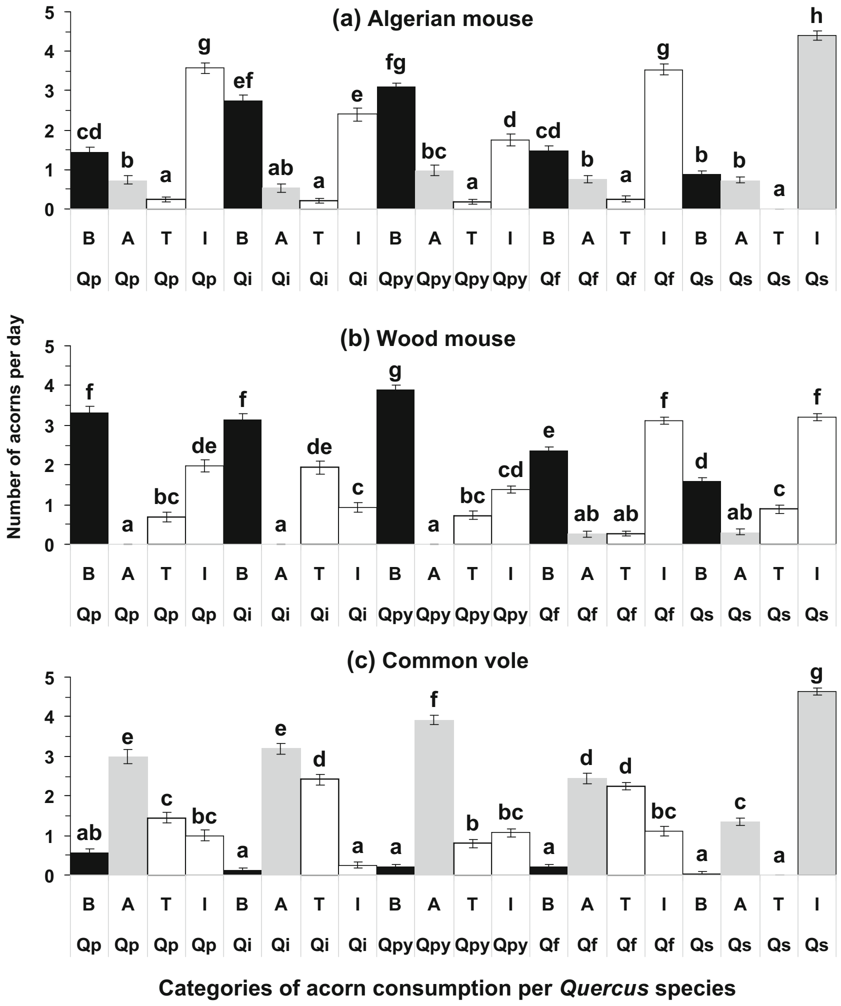

Fig. 1 Average number and standard error of acorns of different *Quercus* species handled by **a** wood mouse, **b** Algerian mouse, and **c** common vole according to the different categories of consumption (B: basal, A: apical, T: totally eaten, I: intact). Different letters above the bars indicate significant differences ($p < 0.05$). See Table 1 for *Quercus* species names and abbreviations

most of the acorns of *Q. petraea*, *Q. pyrenaica*, and *Q. ilex* by the embryo whereas most of *Q. suber* acorns are left intact and if consumed, they are mostly eaten by the embryo (Fig. 1c).

In short, it is observed that it is more frequent that partially eaten acorns of the five *Quercus* species are eaten by the basal end by the wood mouse and the Algerian mouse, whereas the common vole prefers to eat the acorns by the apical end. The highest number of intact acorns belongs to the species *Q. petraea*, *Q. faginea*, and largely to *Q. suber*, which suggests reduced preference for them by the three rodent species under study. Indeed, the absence of significant *Quercus* by rodent interaction (Table 4) suggests that the different rodent species show the same preference for the different *Quercus* species. In general, the three rodent species reject acorns of *Q. suber* and prefer those of *Q. ilex* and *Q. pyrenaica* (Fig. 1).

The LMM analysis also showed a highly significant interaction between "category of consumption," "rodent species," and time (Table 4), suggesting that some of the rodent species modifies over time its way of eating acorns. In particular, only for the common vole, the category of consumption by "time" interaction was significant ($F_{12,\ 800} = 4.35$, $p < 0.001$). The common vole showed a lower consumption of acorns by the apical end the third day, when more acorns remain intact (Fig. 2); no differences along time were found for the other two categories of consumption (basal end, totally eaten).

Discussion

The three rodent species under study showed the same preference for the five species of acorns of *Quercus* species provided. They all rejected acorns of *Q. suber* but consumed acorns of the remaining four *Quercus* species widely distributed on the Iberian Peninsula (*Q. ilex*, *Q. pyrenaica*, *Q. faginae*, and *Q. petraea*). Moreover, there was a significant preference for *Q. ilex* acorns. As suggested by Pons and Pausas (2007) and Sundaram et al. (2015), the criteria for selecting acorns of different *Quercus* species may have a chemical origin. In this case, the three rodent species would behave alike during acorn consumption, as found in our study. The widespread rejection of *Q. suber* (cork oak) acorns, also described by Pons and Pausas (2007), may be due to their higher content of lignin (see

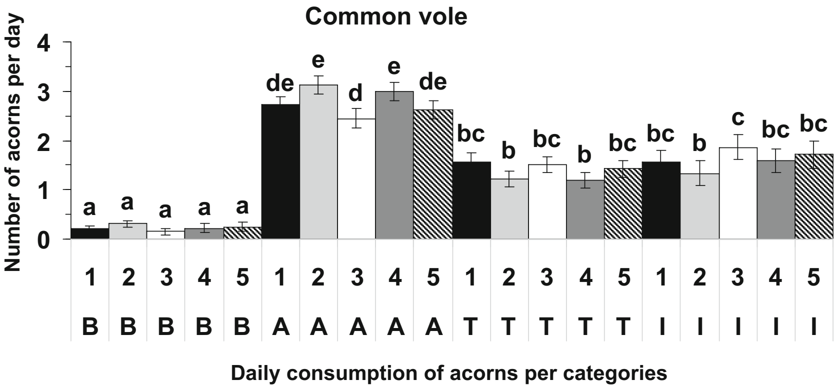

Fig. 2 Average number and standard error of acorns handled per day (1–5) by common vole according to the different categories of consumption (B: basal, A: apical, T: totally eaten, I: intact). Different letters above the bars indicate significant differences ($p < 0.05$)

Table 2). A high lignin content is related to a higher tannin content (De Blas et al. 2003), which, in turn, could deter rodents from eating cork oak acorns (Zhang et al. 2013). Therefore, *Q. suber* acorns may not be widely selected and transported by rodents, and consequently, *Q. suber* would benefit less from the mutualistic relationship with rodents because their acorns were not selected, which could adversely affect their colonization process. On the contrary, the higher fat, protein, and sugar contents of *Q. ilex* acorns (Table 2) could explain the rodents' preference for them, since this is the favorite acorn species eaten by the wood mouse and the Algerian mouse (Pons and Pausas 2007; Muñoz and Bonal 2008a, b; Muñoz et al. 2012; Del Arco and Carretero 2013; Sunyer et al. 2014). This has major implications for ecosystems with a mixture of various *Quercus* species because if *Q. ilex* acorns are the most consumed, they can also be the most widely dispersed and buried, thus gaining an advantage over the unburied acorn species during germination (Muñoz and Bonal 2011; Perea et al. 2012).

Nevertheless, in spite of the uniformity in acorn selection shown by the rodents, their consumption behavior is very different. They all consume many acorns partially but they treat the embryo differently. The two rodent species that habitually eat acorns in their natural habitats (wood mouse and Algerian mouse) consume acorns by the basal part (Del Arco and Carretero 2013), far away from the embryo, thus the embryo remains alive and untouched, able to germinate after burial. In previous experiments, we found that the 15% of the acorns partially eaten from the basal part manage to germinate, which is similar to the germination percentage of intact acorns (JMDA unpublished data). Also, Yang and Yi (2012) found similar percentages of germination for acorns eaten from the basal part (12%) in comparison with intact acorns (13%). On the other hand, the common vole, the rodent species not accustomed to eating acorns (Paz et al. 2012; Luque-Larena et al. 2013), eats acorns by the apical end, the acorn part where the embryo is; the embryo is damaged and acorns are not able to germinate (Steele et al. 2001).

No differences were detected between days insofar as how the two species that usually feed on acorns consumed them, which means that these rodent species do not need to learn to manage them, because their behavior has hereditary character (Muñoz and Bonal 2008b). Despite not having had previous contact with acorns, the subjects begin eating them from the basal part by the previous experience of their ancestors (Chang et al. 2009; Hou et al. 2010; Perea et al. 2012; Yi et al. 2012). Their ancestors have been living among *Quercus* species and eating their seeds for generations. This behavior maintains the mutualistic relationship between the plant and rodent (Sundaram et al. 2015). There is a degree of coevolution between seeds of *Quercus* species and the two scattering rodent species (Zhang et al. 2014). The rodent gets food by eating the surplus part of the acorn. According to Perea et al. (2014) and Yi et al. (2015), acorns have additional reserves greater than what is needed for germination. This could be a strategy to attract dispersing fauna. The plant species, for its part, has its seeds taken to suitable storage locations (Muñoz and Bonal 2011; Perea et al. 2012) where they can germinate although they lack part of the cotyledon (Chang et al. 2009; Yang and Yi 2012; Yi et al. 2012).

On the contrary, the specimens of common vole, which had not had previous contact with acorns, begin to eat them from the apical end, probably for comfort. Nevertheless, they tried different ways of eating the acorns over time (see Table 4, which depicts consumption over time), because they have to learn to deal with a new food with which none of the nine specimens in the experiment nor their ancestors had had contact. Because the way of eating the acorns is not predetermined genetically, this species opens the acorns in the easiest way. We have been able to confirm, by means of recordings, that *M. arvalis* presses the acorns against the soil in order to place it as if it was a missile and then bite it on the narrow end where the embryo is. The other two species, wood mouse and Algerian mouse, avoid the place where the basal end meets the acorn cap, and they start to bite it at its edge (Zhang and Zhang 2008).

Steele et al. (1993) suggest the presence of recalcitrant substances around the embryo, such as tannins, synthesized during fruit ripening, as the cause of rodents eating acorns at the basal end. Nevertheless, Hou et al. (2010) and Yang and Yi (2012) did not find clear differences in the concentration of tannins between the two acorn ends of the species they studied. We did not analyze the tannin content of the different parts of the acorns (basal or apical ends). However, if there really was a higher content of tannins in the area of the embryo and this was the mechanism of rejection, the common vole would have eaten the acorns from the basal part, exactly like the other two rodent species, according to Steele et al. (1993). The fact that common vole preferred to eat acorns from the apical end, as well as its clear rejection of acorns of *Q. suber* (with greater tannin content), suggests that recalcitrant substances do not determine the selection mechanism.

The common vole does not preserve the embryo, and this may have negative implications for the *Quercus* forest regeneration in the study area. This rodent species has invaded the area recently, and it is, for the moment, feeding on its natural food source: crops. However, the species suffers recurring periods of overpopulation that deplete their food. The drought conditions, triggered by climate change, that threaten this Mediterranean region may also drive *M. arvalis* from the areas where crops are grown to the nearby *Quercus* forests. Our study shows that the common vole would not reject the acorns as food source and that their non-hereditary habit of eating acorns from the apical end could arrest the natural regeneration of *Quercus* species, thus limiting forest expansion because of seed destruction.

Conclusion

We conclude that there is a significant difference in the way of consuming the acorns between rodent species used to eat acorns (wood mouse and Algerian mouse) and the expansive species not accustomed to eating acorns (common vole), and it was consistent for the five *Quercus* species used. The three rodent species consume many acorns partially; however, the habitual acorn consumer species (wood mouse and Algerian mouse) eat most of the acorns from the basal end, thus leaving the embryo in place alive and able to germinate. On the other hand, the expansive species, common vole, eats acorns from the apical end; thus, the embryo is damaged and acorns are not able to germinate. The feeding behavior of the two habitual acorn consumer species, wood mouse and Algerian mouse, benefits the mutualistic relation with *Quercus*, probably due to the results of natural selection. The expansive species, common vole, modifies its behavior over time, suggesting that its way of eating the acorns is not genetically fixed. The expansive species, common vole, would impose with time a high risk to the natural regeneration of *Quercus* species in the central plateau, where this species of rodent is expanding in search of food.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international guidelines for the care and use of animals were followed. All procedures performed in this study involving animals were in accordance with the ethical standards of the institution at which the studies were conducted (CEEBA University of Valladolid, Spain). The experimental procedures were designed in accordance with the requirements of replacement, reduction and refinement.

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