

Josep Pons · Juli G. Pausas

Rodent acorn selection in a Mediterranean oak landscape

Received: 4 January 2006 / Accepted: 25 August 2006 / Published online: 7 November 2006
© The Ecological Society of Japan 2006

Abstract *Quercus suber*, *Quercus ilex* and *Quercus coccifera* (Cork, Holm and Kermes oaks, respectively) are common evergreen oak species that coexist in the landscapes of the western part of the Mediterranean basin. Rodents are the main acorn predators and thus one of the main factors for understanding recruitment patterns in oaks. In this paper we analyse to what extent mice prefer acorns from one oak species over another in three oak species studied using acorn removal experiments and video tape recordings. Twenty labelled acorns from each of the three *Quercus* species (60 acorns) were placed in 40 cm×40 cm quadrats on each plot. Because selection might vary as a result of the vegetation context, we performed the trials in the five main vegetation types within the study area (four replicates in each vegetation type) in order to control for habitat influences on rodent acorn preferences (a total of 20 plots). The removal of 1,200 acorns occurred within 68 days. Mice removed 98.7% of the acorns. *Q. ilex* acorns were preferred over *Q. suber* and *Q. coccifera* in all vegetation types except in pine forest, where no acorn preferences were detected. Acorn removal rates differed with vegetation type, correlating positively with shrub cover. The distance at which acorns were displaced by rodents (mean = 4.6 m ± 5.1 SD) did not differ between acorn species, but varied among vegetation types. Bigger acorns of *Q. coccifera* were selected only after *Q. ilex* and *Q. suber* acorns were depleted, while no size selection was detected for the latter two species. Thus, we conclude that rodents show preference for some

oak acorns and that landscape context contributes significantly to rodent activities and decisions.

Keywords *Apodemus sylvaticus* · *Quercus coccifera* · *Quercus ilex* · *Quercus suber* · Removal rates · Retrieval distances · Size selection

Introduction

Many Mediterranean landscapes are dominated by oak (*Quercus*) species, especially evergreen oaks. In the Mediterranean basin, evergreen oaks of different species can coexist, forming mixed forests with pines, appearing in the understory or being dominant in some shrubland communities (garrigue). This oak spatial diversity may be related to different resource requirements, disturbance responses or past uses (Mohler 1990). These different communities with varying oak abundance can be found as mosaics of Mediterranean landscapes (mixed oak landscapes), and thus acorns from different oak species (sympatric acorn-producing species) may be available to predator populations. Furthermore, acorns are a very valuable food source for rodents (Jensen 1985), and rodents are the main acorn predators (Shaw 1968).

It has been suggested that acorn crop variability may affect mouse populations the following spring and summer (Mcshea 2000), but the role of species-specific seed preferences by rodents (Ivan and Swihart 2000; Shimada 2001a; Sone and Kohno 1996) is still unknown. Although the total inter-specific variation in acorn production has been recognised to have a great influence on seed eaters (Liebhold et al. 2004), few studies have dealt with the differential selective pressure by these seed eaters on the producers' actual performance (i.e., mast and regeneration patterns, but see Hoshizaki and Hulme 2002).

It has been suggested that rodents have a preference for large acorns from Holm oak *Quercus ilex* (Gomez 2004a); however, in mixed oak landscapes, acorns of

J. Pons · J. G. Pausas (✉)
CEAM Fundación Centro de Estudios Ambientales del
Mediterráneo, C. Charles Darwin 14, Paterna,
46980 Valencia, Spain
E-mail: juli@ceam.es
Tel.: +34-96-1318190

J. G. Pausas
Departament d'Ecologia, Universitat d'Alacant,
Ap. Correus 99, 03080 Alacant, Spain

different species may vary not only in size, but also in nutritional properties (Ferreira-Dias et al. 2003; Shimada 2001b; Talebbendiab et al. 1991) and tannin levels (Cantos et al. 2003). The question that arises is to what extent rodents show a preference for acorns of a given oak species. Differential acorn selection may produce changes in predation pressure and dispersal rates in different oak species (Shimada 2001a; Stapanian and Smith 1978) and have evolutionary implications on the differential mast seeding dynamics or community oak species composition (Janzen 1971).

Rodents suffer higher predation risk in areas with reduced vegetation cover of low height (Kollmann 1995; Manson and Stiles 1998). Therefore, rodent activity, rodent population densities or rodent species composition may differ between more open habitats and shrubby habitats (Falkenberg and Clarke 1998). As a consequence, if rodents select acorn types (i.e., species or size), the degree of selection and/or other variables in the acorn predation mechanisms could differ as a function of the surrounding vegetation. Rodent differential seed predation has been documented in Fagaceae species for both temperate forests and indoor trials (Briggs and Smith 1989; Shimada 2001a). To our knowledge, no such studies have been carried out in Mediterranean landscape mosaics under field conditions.

Thus, our objectives are: (1) to determine if mice prefer any of the acorns tested over the others and (2) to quantify any variation in acorn removal rates and displacement distances as a function of the vegetation type. Our hypothesis is that rodents are the main predators and that they select for nutritionally superior acorns. These acorns would be transported farther because of the higher nutritional revenue. However, this pattern would vary with respect to the different vegetation types because of different rodent density, predation risk, food availability and/or percent of available places to cache acorns. To test this hypothesis, we performed an experiment in which labelled acorns from three oak species were placed in five different vegetation types and left for depletion by rodents. Video recordings were also used for complementing the analyses.

Materials and methods

Study area

The study was performed in the Espadà mountains, eastern Iberian Peninsula (39°51'N, 0°20'W, close to Chovar, Castelló province). The climate is typically Mediterranean with summer drought and mild and wet winters. Two bedrock types are common, Bundsandstein sandstone (the most common) and limestone. The vegetation is the product of a long history of fire and land use, in which many slopes were terraced and cultivated in the past, and then abandoned (Pausas 2004; Bonet and Pausas 2006). Thus, current landscapes are mosaics of five main vegetation types: Holm oak forests (HF)

(forests dominated by *Q. ilex* subsp. *rotundifolia*), Cork oak forests (CF) (dominated by *Quercus suber*), Kermes oak garrigue (GA) (shrublands dominated by *Quercus coccifera*), pine forests (dominated by *Pinus halepensis* and/or *Pinus pinaster*) and abandoned fields (at different abandonment ages). The three oaks, Holm oak, Cork oak and Kermes oak, are evergreen species; the first and second are trees and the third is a shrub.

The wood mouse (*Apodemus sylvaticus*) and Algerian mouse (*Mus spretus*) are the dominant rodents in the study area. Previous field trap sessions found that the population of the latter is about a third of the former and that the black rat (*Rattus rattus*) is present at much lower densities (own unpublished data).

Sampling

Four replicate plots were located in each of the five different vegetation types (therefore, 20 plots): HF, CF, GA, pine woodland (PF) and oldfields (OF, abandoned fields currently covered by shrubs and grasses, without oaks). These vegetation types were selected because they are the dominant landscape units in the study area. For plot characterisation, a plot size of 10 m×10 m was considered; however, acorns removed from the centre of the plot (removal experiment, see below) were searched for without considering plot size. Vegetation on each plot was characterised by using four 10-m transects along the main cardinal directions and recording species occurrence and height every 33 cm. Because the objective of the habitat characterisation was to look for variables explaining different acorn predation rates, the cover percentages of structures relevant to rodents were recorded as well (bare soil, fallen branches, stones and terrace walls). Additional plot characteristics (aspect, slope, tree cover, grazing symptoms and bedrock type) were also recorded.

In autumn 2003, acorns of the three oak species were obtained from several trees in the study area or nearby populations and stored in a constant-cold humidity chamber. Nonviable and unripe acorns were discarded by the floating method and visual screening. In spring 2004, 20 acorns from each of the three oak species, *Q. ilex* subsp. *rotundifolia* (Qi), *Q. suber* (Qs) and *Q. coccifera* (Qc), were placed in a 40 cm×40 cm quadrat in the centre of each plot (therefore, 1,200 acorns). The quadrats were surrounded with coloured powder to be able to identify predator footprints. Acorns were labelled for their identification with a numbered plastic label tied on with a thin iron string (Xiao et al. 2004; mean weight of labels 0.54 ± 0.01 g, $n = 10$). To monitor acorn removal, plots were periodically visited: first every 2 days, then every week and finally at 2-week intervals. On each visit, the labels were searched out and mapped; the status of the acorn (unaffected, eaten or partially eaten) was also recorded. Two plots were depleted in just 1 night; although these plots provided information on the total removal rate, they did not offer information on

rodent acorn species preferences. Moreover, in order to increase the power of the survival function through ties multiplications, we found it necessary to reduce the time interval to rank cases (Muenchow 1986) as a synchronic approach. Thus, a total of four films (each of 3 h in length) were recorded at two plots (one in an OF and the other in a shrubland). In films 1 and 4, the species of some predated acorns could not be identified and were classified as 'unknown species'.

To assess whether rodents select acorn sizes, all acorns corresponding to Cork forest habitat (sites 17, 18, 19 and 20) were previously weighed (0.1 mg precision). The mean weight of the acorn plus tag was $4.18 \text{ g} \pm 1.09 \text{ SD}$ ($n=240$, range 2.5–9.0 g). By species, Qi and Qs acorns were similar ($4.44 \text{ g} \pm 0.98 \text{ SD}$ and $4.70 \text{ g} \pm 1.17 \text{ SD}$, respectively) and approximately 1 g heavier than Qc acorns ($3.46 \text{ g} \pm 0.46 \text{ SD}$; ANOVA for species mean weight differences, $F=40.621$, $df=2$, $P<0.001$).

The experiments were performed in spring (that is, outside the peak acorn-drop period) to avoid interference in the selection behaviour by the natural levels of acorn abundance on each site, that is, to avoid the possible differential masting and relative abundance of oak species on each site. This implies that our results may reflect the intrinsic behaviour of the predators (as in a lab experiment) more than their behaviour under natural conditions, which may be too heterogeneous to allow easy interpretation of the results.

Data analysis

Acorn removal

Median removal time, i.e., the time at which 50% of the acorns were removed (hereafter MRT and expressed in days), was used to compare acorn removal rates in both the vegetation type \times acorn species experiment and in the films. Survival function analysis (time failure analysis, Pyke 1986) was used to analyse acorn removal rates, taking into account both vegetation type and acorn species. By 'survival', we refer to acorns not removed from the 40 cm \times 40 cm quadrat (i.e., remaining in the quadrat). Cox regression was used to control for factor variance and was tested with Gehan's generalised Wilcoxon test (hereafter Wilcoxon).

Video monitoring of acorn removal

Time failure analysis and Cox regression were also used to analyse acorn removal rates by species. However, because of the limited length of the video tapes, in many cases fewer than 50% of the removed acorns were filmed, and thus, MRT was not computed. Alternatively, Ivlev's Electivity Index (Scarlett and Smith 1991) was used to quantify rodent preference for a particular acorn species in the video monitoring. Electivity is

calculated for each acorn species as $E_i=(R_i - P_i)/(R_i + P_i)$, where R_i is the number of acorns of the species i selected and P_i is the number of acorns of the species i supplied. This electivity index ranges from -1 to 1 , with negative values indicating avoidance and positives values indicating selection.

Acorn size

Acorn weight was tested in the Cork oak vegetation type, and data were grouped between the acorns removed on the day following the beginning of the experiment (early removal) and those removed afterwards (late removal). A univariate ANOVA procedure (GLM module, SPSS 10.5) was used to compare acorn weight and retrieval distances (log-transformed).

Distances of tag retrieval

Tag retrieval distance (TRD) was measured as the distance (straight line) from the quadrat to the place where the label was found, usually a few days after removal, for both eaten and not-eaten acorns. We did not consider cache relocations in this study. To compare the different TRD distribution between vegetation types and between acorn species we used the non-parametric median test. In the cases where it was significant, we performed the pairwise comparisons using the Kolmogorov–Smirnov test (K–S test); both tests compare the full distribution of distances.

Determinants of removal rates

Stepwise forward multiple regression was used to reveal the significant plot variables that explained most of the variability in MRT (log-transformed prior to the analysis). The initial variables included in the regression model were the parameters obtained from the transects (mean vegetation height, standard deviation in vegetation height, plant cover and a structural diversity index) and aspect. The structural diversity index was computed as the Simpson's diversity index (Simpson's D), including plant species and physical structures relevant to rodents (such as rocks, bare soil and dead branches). For computing Simpson's D , species accounting for less than 5% of total cover or species present on only one site were aggregated into the category 'others'. Plant cover was computed for different strata: ground level (<20 cm), short shrubs (20–50 cm), medium shrubs (50–120 cm), tall shrubs (120–300 cm) and tree layer (>300 cm). Aspect was transformed in an aspect index (AI), which was computed as: $AI = \cos(\alpha - 22.5)$, where α is the aspect angle in decimal degrees (Pausas et al. 2004). This transformation is necessary to account for the more mesic conditions of the north–east aspect as most of the humidity in the study region comes from the Mediterranean sea (eastwards).

Results

Acorn removal

Track prints in the quadrats revealed that rodents were the main acorn predators. However, differentiating between the two species in the study area (*A. sylvaticus* and *M. spretus*) on the basis of their tracks was extremely difficult, and no attempt was made to quantify them. Only on two plots did other vertebrates (jays and domestic sheep) predate a few acorns (1.6% of total), and these data were omitted from the analysis. Rodents took on average 8.8 nights to discover the acorns (range 1–34 nights) and an additional 11.4 nights (on average) to remove all the acorns (range 1–57 nights). After 68 days, no acorns were left in the quadrats. Acorn removal was higher immediately after the plot was discovered and decreased with time: after 1 week more than 50% of acorns had disappeared (MRT=6.3 days), and after 2 weeks this percentage was about 75%.

The median removal time differs between vegetation types (Wilcoxon statistic=287.822, $df=4$, $P<0.001$) and was shortest on OF (MRT=1.6 days), longest on PF (MRT=18.5 days) and intermediate in the remaining vegetation types (MRT=5–8 days; Table 1). MRT also varied with the acorn species considered (Wilcoxon statistic=9.375, $df=2$, $P=0.009$). Qi acorns were removed faster (MRT=5.8 days) than Qs and Qc acorns (MRT=6.5–6.8 days; Table 1). However, acorn species \times vegetation type interaction was also significant: Qi acorns were positively selected on HF, CF and GA, but no acorn preferences appear on PF and OF. Very fast removal rates (i.e., removal of all acorns in just 1 night) prevented any acorn species selection evidence in OF. However, the video films revealed a Qi preference over the others (see below) in OF.

Table 1 Median removal time (MRT, in days) values by vegetation type and acorn species

	Removal time (days)		
	MRT	<i>n</i>	<i>P</i>
Vegetation types			
HF	5.1	240	b
CF	5.8	240	c
GA	8.0	240	d
PF	18.5	240	e
OF	1.6	240	a
Overall			<0.001
Acorn species			
Qi	5.8	400	a
Qs	6.8	400	b
Qc	6.5	400	b
Overall			0.009
Overall	6.3	1,200	

In *P*, letters refer to Bonferroni-corrected pairwise comparisons at $P<0.05$ significance level, while numbers refer to the significance of the Wilcoxon test

Video monitoring of acorn removal

Because of the limited tape length (3 h), only the first 21.7–58.3% of the removed acorns were filmed (total $n=240$) in a total of four film sessions. We found differences in removal rates between the different acorn species (Table 2). Qi acorns were preferred in all films, ranging between 47.6 and 61.5% of the total removed acorns filmed (mean 55%), followed by Qs (24%) and Qc (21%) (Table 2). Qi acorns were removed more than Qc acorns, and more than Qs acorns (Table 2), and no acorn selection seems to occur between the latter two acorns species (Table 2). In accordance, the electivity index was positive for Qi and negative for Qs and Qc, being the lowest in Qc (Table 2).

Acorn size

Plots 17, 18 and 19 were depleted after two to three visits to the plot (6–7 nights); because plot 20 was depleted in just 1 night, it was not considered for further analysis. We grouped the data as a function of removal time ('early' for acorns removed on the first visit, and 'late' for acorns removed on the second or third visit) and analysed the three acorn species separately as they differ in weight. Mean acorn plus tag weight did not differ between groups for either Qi (early = 4.69 ± 0.72 g, $n=14$; late = 4.38 ± 1.10 g, $n=46$; Table 3) or Qs (early = 4.83 ± 1.29 g, $n=28$; late = 4.43 ± 1.17 g, $n=32$; Table 3). On average, a significant difference of 0.2 g was detected between the early and late Qc acorn groups (early, mean weight = 3.62 ± 0.48 g, $n=20$; late, mean weight = 3.40 ± 0.48 g, $n=40$; Table 3) and marginal significance for the group (early/late) \times plot interaction (see Table 3). Since acorn size is directly proportional to acorn weight, these results indicate some preference by rodents for bigger Qc acorns, but no size discrimination for Qi or Qs acorns. No significant correlation was

Table 2 Overall results on acorn removal in the four films, including the number of initial and removed acorns, the electivity index, the pairwise comparisons for differences in the estimated survival functions for each acorn species and the pairwise comparisons for the mean electivity index (only significant differences are shown)

	Number of acorns	Mean electivity (SE)
Initial acorns for each species	80	
Acorns removed by species		
Qi	55	0.424 (0.021)
Qs	24	-0.357 (0.029)
Qc	21	-0.417 (0.031)
Total acorns tracked	100	
Significant pairwise comparisons (Wilcoxon test)		
Qi–Qs	23.07 ($P<0.0001$)	9.178 ($P<0.001$)
Qi–Qc	27.35 ($P<0.0001$)	8.928 ($P<0.001$)

Table 3 ANOVA analysis of acorn weight as dependent factor and plot and removal group (early or late) as main factors

Acorn sp.	Source	MS	df	F	Significance
Qi	Plot	218.240	2	2.330	0.107
	Group	34.300	1	0.366	0.548
	Plot × group	54.081	2	0.577	0.565
	Error	93.661			
Qs	Plot	80.578	2	0.516	0.600
	Group	186.150	1	1.191	0.280
	Plot × group	91.099	2	0.583	0.562
	Error	156.261			
Qc	Plot	16.315	2	0.744	0.480
	Group	98.532	1	4.492	0.039*
	Plot × group	63.733	2	2.905	0.063!
	Error	21.936			

Analysis was run independently for each acorn species (see text for further details)

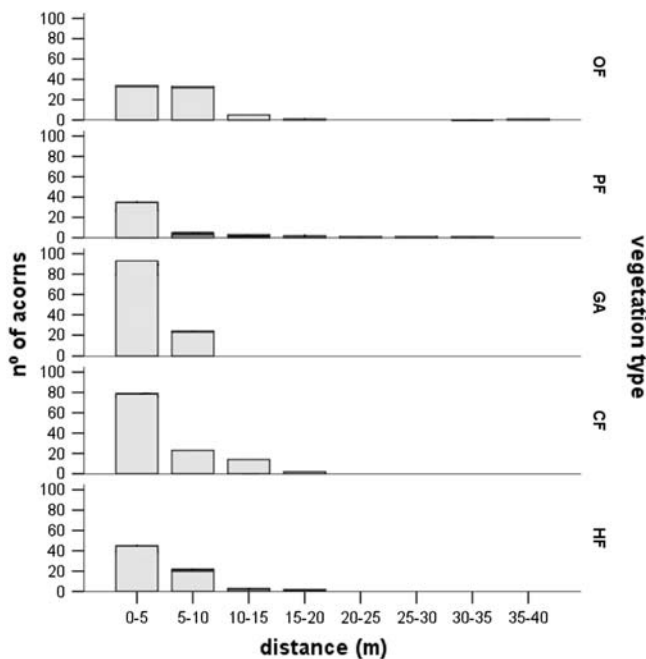


Fig. 1 Frequency distributions of TRDs by vegetation type: *OF* oldfields, *PF* pine forest, *GA* garrigue, *HF* Holm oak forest, *CF* Cork oak forest

found between the TRD and acorn-tag weight (Pearson correlation = -0.022 , $P = 0.809$, $n = 119$).

Distances of tag retrieval

Mean TRD was 4.6 m (SD = 5.1), with a maximum of 62 m on an OF. However, these values should be considered underestimations as only 36% of the tags were located. This is probably because the effort involved in locating long-distance tags increases exponentially, and some of the lost tags would correspond to long-distance

movements. No acorn species differences were found in the percent of acorn label retrieval ($Q_i = 33.9\%$, $Q_s = 34.1\%$, $Q_c = 31.5\%$, $n = 1,154$, $F = 0.339$, $P = 0.713$).

Tag retrieval distance differed between vegetation type (median test, $\chi^2 = 23.287$, $df = 4$, $P < 0.001$, $n = 431$). Pairwise comparisons (K–S test) indicate that TRD was longer in OF (mean = 6.7 ± 7.4 m, maximum = 62.0, $n = 74$), shorter in garrigue (mean = 3.3 ± 1.8 m, maximum = 7.5, $n = 118$), Holm (mean = 4.6 ± 3.4 m, maximum = 18.4, $n = 72$) and CF (mean = 4.0 ± 4.1 m, maximum = 16.3, $n = 119$) and intermediate in pine forest (mean = 6.3 ± 8.7 m, maximum = 40.1, $n = 48$) (Fig. 1). All pairwise comparisons between vegetation types were significant at the $P < 0.03$ level (K–S test) except for and GA–PF ($P = 0.07$).

When considering acorn species, no significant differences in TRD were found for the whole population (median test, $\chi^2 = 2.417$, $df = 2$, $n = 431$, $P = 0.299$). The maximum TRD for Q_s (62.0 m, $n = 149$) was remarkably larger than for Q_c (18.6 m, $n = 151$).

Determinants of removal rates

At plot scale (20 plots), the stepwise regression was selected as the best fit for MRT the model with medium shrub (50–120 cm) and the SD of vegetation height (vertical complexity). MRT shows a negative relation with both parameters ($\log \text{MRT} = 2.715 - 1.772 \times \text{medium shrub cover} - 0.012 \times \text{vegetation height SD}$; cover was arcsine-root transformed, adjusted $R^2 = 0.485$, $P = 0.001$). That is, mice remove quicker in sites with greater shrub cover and vertical complexity, which corresponds to shrublands, long abandoned OF and shrubby oak forest. For TRD, a significant, but weak relation was found with short shrub (20–50 cm) cover ($\log \text{TRD} = 0.840 - 0.016 \times \text{short shrub cover}$, adjusted $R^2 = 0.19$, $P = 0.032$), suggesting greater acorn movements in sites with high short vegetation cover, usually corresponding to recently abandoned OF and pine forest sites.

Discussion

Rodents were the main agents in the acorn removal, as has been reported in other Mediterranean landscapes (Alcantara 2000; Gomez et al. 2003; Borchert 1989), and they clearly selected Q_i acorns. Preferences for Q_i acorns could be related to their higher nutritional value in terms of oil content (7.3–9.1% relative to $Q_s = 5.0$ –5.2%; Talebbendiab et al. 1990, 1991; Afzalrafii et al. 1992; Nieto et al. 2002; Ferreira-Dias et al. 2003) or to their lower content in tannins relative to Q_c (Cañellas and San Miguel 2003), or probably to both. Higher tannin content indirectly implies lower nutritional value because energy is needed to neutralise the tannin (Janzen 1971). The selection of Q_i over Q_s could be partially explained by the high phenolic compound content in the

Qs acorn skin (Cantos et al. 2003), but it is still unknown whether this substance acts as a signal cue or has an effect over rodents by itself. Species preferences could not be related to synchronic exposure to different acorn densities because the field experiments were carried out in March when natural acorn production does not occur.

At least in CF, rodents removed Qi and Qs acorns independently of their size, while for Qc, they chose large acorns. The Qc acorns used in our trials were smaller than those of the other species, and this might have contributed, to some extent, to the selection of the larger Qc acorns. The absence of acorn-size selection reported by Xiao et al. (2004) seems to be in conflict with results from other studies (Alcantara 2000; Gomez 2004a). However, our results suggest that size selection could be species-dependent (i.e., seed quality). Differences in acorn location may contribute to the differences between our results (from acorns set at the soil surface) and those from Gomez (2004a; buried acorns), because detectability and time to remove the acorns may be longer in buried acorns.

Rodent preferences for different acorns can be divided into feeding and carrying/hoarding preferences (Shimada 2001a). We have not tested these separately, but the lack of differences in TRDs suggests that Qi preference is set at the experimental depot site. However, the fact that Qc acorns were found attached to the tag more often than expected (data not shown) suggests that Qi and Qs acorns were preferred for feeding and that, afterwards, Qc acorns were moved for storage. Alternatively, the preferred acorns could have been better hidden, thus making it harder for us to locate (i.e., sampling error). To solve this problem, more accurate acorn-tracking methods (Sone and Kohno 1996; Hoshizaki and Hulme 2002) should be used.

Removal rates, acorn species preference and TRD varied with the vegetation type considered. Vegetation structure (mostly shrub cover) accounts for part of these differences in agreement with previous studies (Díaz 1992; Kollmann 1995), but food availability and rodent community composition—species and relative densities—could also be important (Ostfeld et al. 1997). In relation to vegetation type, we have found three clear patterns: (1) mice Qi preference is observed in all the vegetation types except in PF. A probable reason for this pattern is a high mice predation risk in pine forests (i.e., shorter time for acorn discrimination and selection; Willson and Whelan 1990; Hulme 1994, 1997; Alcantara 2000; Torre and Díaz 2004; Díaz et al. 2005). (2) Acorn removal rates are higher in OF and lower in PF (intermediate in HF, CF and GA). This seems to be related to shrub cover and vegetation structure. This pattern is in agreement with higher mice densities deduced from live-trapping under increasing shrub cover (unpublished data) and with the *Quercus* recruitment densities (Pons and Pausas 2006). (3) TRDs increase from GA to OF and PF (HF and CF intermediate). An explanation for this pattern is difficult as TRD showed a weak correla-

tion with short shrub cover. The greater acorn movement distances in OF and PF might be the result of different causes such as the lack of safe sites in PF or the high mice densities in OF (e.g., longer distance movements for reducing pilfering by congeners; Vander Wall 2002).

Most of the literature deals with just one acorn species (Shaw 1968; Herrera 1995; Gomez et al. 2003; Gomez 2004a, b; Pulido and Díaz 2005). However, most vertebrates that consume acorns interact with several acorn species at the same time. Our finding of Qi preference over Qs and Qc might have implications for differential recruitment in a mixed oak population. However, prior to extracting the direction of this selection on the population dynamics of the different *Quercus* species, we must deal with the possible variation because of a specific *Quercus* masting pattern and with the relationship between mice populations and the last year's acorn availability (see, i.e., Ostfeld et al. 1996). We suggest that the predator–disperser activity of mice would be different not only because of the vegetation type and the previous year's acorn production, but also because of the preferences of mice for specific acorns. In other words, under specific conditions mice could act as a disperser for some acorns and as a predator for others.

Acorn predation is one of the multi-steps in oak recruitment. Probably extending the multi-species approach to the whole oak regeneration process will yield some promising results.

Acknowledgments This work has been financed by the EU project CREOAK (QLRT-2001-01594) and the Spanish project VARQUS (CGL2004-04325/BOS). T. Rodrigues and P. Azeiteiro helped with the field work under an EU Leonardo da Vinci fellowship. We thank M. Díaz, A. Muñoz and J. Belliure for their kind review of the first draft of this paper. CEAM is funded by *Generalitat Valenciana* and *Bancaixa*.

References

- Afzalrafi Z, Dodd RS, Pelleau Y (1992) Mediterranean evergreen oak diversity—morphological and chemical variation of acorns. *Can J Bot* 70:1459–1466
- Alcantara JM (2000) Factors shaping the seedfall pattern of a bird-dispersed plant. *Ecology* 81:1937–1950
- Bonet A, Pausas JG (2006) Old field dynamics on the dry side of the Mediterranean basin: patterns and processes in semiarid SE Spain. In: Cramer VA, Hobbs RJ (eds) *Old fields: dynamics and restoration of abandoned farmland*. Island Press (in press)
- Borchert M (1989) Interaction of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. *Ecology* 70:389–404
- Briggs JM, Smith KG (1989) Influence of habitat on acorn selection by *Peromyscus leucopus*. *J Mammal* 70:35–43
- Cañellas I, San Miguel A (2003) La coscoja (*Quercus coccifera* L.): ecología, características y usos. Monografías. INIA, Madrid
- Cantos E, Espin JC, Lopez-Bote C, De la Hoz L, Ordóñez JA, Tomas-Barberan FA (2003) Phenolic compounds and fatty acids from acorns (*Quercus* spp.), the main dietary constituent of free-ranged Iberian pigs. *J Agric Food Chem* 51:6248–6255
- Díaz M, Torre I, Peris A, Tena L (2005) Foraging behaviour of wood mice as related to presence and activity of genets. *J Mammal* 86:165–172

- Falkenberg JC, Clarke JA (1998) Microhabitat use of deer mice: effects of interspecific interaction risk. *J Mammal* 79:558–565
- Ferreira-Dias S, Valente DG, Abreu JMF (2003) Pattern recognition of acorns from different *Quercus* species based on oil content and fatty acid profile. *Grasas y Aceites* 54:384–391
- Gomez JM (2004a) Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. *Evolution* 58:71–80
- Gomez JM (2004b) Importance of microhabitat and acorn burial on *Quercus ilex* early recruitment: non-additive effects on multiple demographic processes. *Plant Ecol* 172:287–297
- Gomez JM, Garcia D, Zamora R (2003) Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. *For Ecol Manage* 180:125–134
- Hoshizaki K, Hulme PE (2002) Mast seeding and predator-mediated indirect interactions in a forest community: evidence from post-dispersal fate of rodent-generated caches. In: *Seed dispersal and frugivory*. CAB International, UK, pp 227–239
- Hulme PE (1994) Post dispersal seed predation in grassland: its magnitude and sources of variation. *J Ecol* 82:645–652
- Hulme PE (1997) Post-dispersal seed predation and the establishment of vertebrate dispersed plants in Mediterranean scrublands. *Oecologia* 111:91–98
- Ivan JS, Swihart RK (2000) Selection of mast by granivorous rodents of the central hardwood forest region. *J Mammal* 81:549–562
- Janzen DH (1971) Seed predation by animals. *Annu Rev Ecol Syst* 2:465–492
- Jensen TS (1985) Seed-seed predator interactions of European beech (*Fagus sylvatica*) and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. *Oikos* 44:149–156
- Kollmann J (1995) Regeneration window for fleshy-fruited plants during scrub development on abandoned grassland. *Ecoscience* 2:213–222
- Liebold A, Sork V, Peltonen M, Koenig W, Bjornstad ON, Westfall R, Elkinton J, Knops JMH (2004) Within-population spatial synchrony in mast seeding of North American oaks. *Oikos* 104:156–164
- Manson RH, Stiles EW (1998) Links between microhabitat preferences and seed predation by small mammals in old fields. *Oikos* 82:37–50
- McShea WJ (2000) The influence of acorn crops on annual variation in rodent and bird populations. *Ecology* 81:228–238
- Mohler CL (1990) Co-occurrence of oak subgenera: implications for niche differentiation. *Bull Torrey Bot Club* 117:247–255
- Muenchow G (1986) Ecological use of time failure analysis. *Ecology* 67:246–250
- Nieto R, Rivera M, Garcia MA, Aguilera JF (2002) Amino acid availability and energy value of acorn in the Iberian pig. *Livest Prod Sci* 77:227–239
- Ostfeld RS, Jones CG, Wolff JO (1996) Of mice and mast. *Bio-science* 46:323–330
- Ostfeld RS, Manson RH, Canham CD (1997) Effects of rodents on survival of tree seeds and seedlings invading old fields. *Ecology* 78:1531–1542
- Pausas JG (2004) Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Clim Change* 63:337–350
- Pausas JG, Blade C, Valdecantos A, Seva JP, Fuentes D, Alloza JA, Vilagrosa A, Bautista S, Cortina J, Vallejo R (2004) Pines and oaks in the restoration of Mediterranean landscapes of Spain: new perspectives for an old practice—a review. *Plant Ecol* 171:209–220
- Pons J, Pausas JG (2006) Oak regeneration in heterogeneous landscapes: the case of fragmented *Quercus suber* forests in the eastern Iberian Peninsula. *For Ecol Manage* 231:196–204
- Pulido FJ, Diaz M (2005) Regeneration of a Mediterranean oak: a whole-cycle approach. *Ecoscience* 12:92–102
- Pyke DA (1986) Statistical analysis of survival and removal rates experiments. *Ecology* 67:240–245
- Scarlett TL, Smith G (1991) Acorn preference of urban Blue Jays (*Cyanocitta cristata*) during fall and spring in north-eastern Arkansas. *Condor* 93:438–442
- Shaw MW (1968) Factors affecting the natural regeneration of Sessile oak (*Q. petraea*) in North Wales: acorn losses and germination under field conditions. *J Ecol* 56:647–659
- Shimada T (2001a) Hoarding behaviors of two wood mouse species: different preference for acorns of two *Fagaceae* species. *Ecol Res* 16:127–133
- Shimada T (2001b) Nutrient compositions of acorns and horse chestnuts in relation to seed-hoarding. *Ecol Res* 16:803–808
- Sone K, Kohno A (1996) Application of radiotelemetry to the survey of acorn dispersal by *Apodemus* mice. *Ecol Res* 11:187–192
- Stapanian MA, Smith CC (1978) A model for seed scatterhoarding: coevolution of fox squirrels and black walnuts. *Ecology* 59:884–896
- Talebendjab SA, Benmahdi M, Mashev NP, Vassilev GN (1990) Contribution to the investigation of the chemical composition of the acorn of various *Quercus* species in Algeria—investigating the acorn of *Quercus ilex*. *Dokl Bolg Akad Nauk* 43:83–86
- Talebendjab SA, Benmahdi M, Mashev N, Vassilev GN (1991) A tribute to the study of the chemical composition of the acorn of different species of *Quercus* spread in Algeria. *Dokl Bolg Akad Nauk* 44:85–88
- Torre I, Diaz M (2004) Small mammal abundance in Mediterranean post-fire habitats: a role for predators? *Acta Oecol* 25:137–142
- Vander Wall SB (2002) Masting in animal-dispersed pines facilitates seed dispersal. *Ecology* 83:3508–3516
- Willson MF, Whelan CJ (1990) Variation in postdispersal survival of vertebrate dispersed seed: effects of density, habitat, location, season and species. *Oikos* 57:191–198
- Xiao ZS, Zhang ZB, Wang YS (2004) Dispersal and germination of big and small nuts of *Quercus serrata* in a subtropical broad-leaved evergreen forest. *For Ecol Manage* 195:141–150