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Fragmentation modifies seed trait effects on scatter-hoarders' foraging decisions

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Abstract Scatter-hoarding animals are crucial in seed dispersal of nut-bearing plants. We used the holm oak *Quercus ilex*—wood mouse *Apodemus sylvaticus* mutualism as a model system to evaluate the relative importance of seed size and fat content on scatter-hoarders' foraging decisions influencing oak dispersal and potential recruitment. We performed a field experiment in which we offered holm oak acorns with contrasting seed size (2 vs 5 g) and fat content (3 vs 11%). Moreover, to test if the strength of these seed trait effects was context-dependent, experimental acorns were placed in small fragments, where natural regeneration is scarce or absent, and forest habitats. In small fragments, rodents had to face increased intraspecific competition for acorns and reduced anti-predator cover during transportation. As a result, they became more selective to ensure rapid acquisition of most valuable food items but, in turn, transported seeds closer to avoid unaffordable predation risks. During harvesting and caching, larger acorns were prioritized and preferentially cached. Fat content only had a minor effect in harvesting preferences. In contrast, in forest sites, where rodent abundance was four times lower and understory cover was well-developed, rodents were not selective but provided enhanced dispersal services to oaks (caching rates were 75% higher). From the plants' perspective, our results imply that the benefits of producing costly seeds are context-dependent. Seed traits modified harvesting and caching rates only when rodents were forced to forage more efficiently in response to increased intraspecific competition. However, when landscape traits limited cache protection strategies, a more selective foraging behavior by scatter-hoarders did not result in enhanced dispersal services. Overall, our result shows that successful dispersal of acorns depends on how specific traits modulate their value and how landscape properties affect rodents' ability to safeguard them for later consumption.

Keywords Acorn dispersal fragmentation · Size · Fat · Competition · Risk

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Introduction

Scatter-hoarding animals are crucial in seed dispersal of nut-bearing plants (Vander Wall 1990). From the animals' view, storing seeds in individual caches allows them to equalize food availability over space, and most importantly, over time ensuring food supply during periods of scarcity. From the plants' perspective, transportation and burial reduce seed predation close to source trees and maintain seed viability over longer periods of time (Vander Wall 2001; Gómez et al. 2008).

Among scatter-hoarders, rodents often dominate local dynamics of forest regeneration (Jansen et al. 2004; Gómez et al. 2008; Pesendorfer et al. 2016) and may become the only seed dispersers in anthropogenic landscapes (Morán-López et al. 2015). Thus, a better understanding of the behavioral mechanisms driving rodents' foraging decisions will provide valuable information about seed dispersal and regeneration patterns of nut-bearing plants. Scatter-hoarding can be viewed as a step-wise process that begins when an animal encounters a seed and ends when the animal decides where and when to consume it. It can be divided into four consecutive stages where the hoarder decides whether (1) to ignore or manipulate an encountered seed; (2) to carry it away or consume it in situ; (3) upon removal, how far to carry it; and (4) to eat or cache the transported seed (Wang et al. 2013). During this process, animals balance the costs and benefits of each foraging decision according to their internal motivations, seed traits, and environmental factors (Lichti et al. 2017).

Regarding seed traits, size and nutrient rewards affect hoarders' foraging decisions. In general, larger seeds are harvested more rapidly, transported further and preferentially stored (e.g. Gómez et al. 2008; Pérez-Ramos et al. 2008; Wang and Chen 2008, 2009; Perea et al. 2012; Sunyer et al. 2014). All else being equal, larger seeds contain more energy and nutrients (Jansen et al. 2004). Thus, by preferentially harvesting and caching them, rodents rapidly sequester the most valuable food items whereas by transporting them further they decrease cache pilferage risks (Lichti et al. 2017). Among nutrients, fat is tightly linked to energy-intake optimization strategies, and it is a fundamental component of mammals' diet (Wang and Chen 2012). Like larger seeds, fat-rich seeds are usually removed faster (Xiao et al. 2006b; Wang et al. 2013; Wang and

Yang 2014). However, fat content effects on dispersal patterns (distance and caching rates) are less clear (Wang and Yang 2014; Lichti et al. 2017). Therefore, maintaining other traits constant, larger and fat-rich seeds are expected to be preferentially removed and stored, and hence, to show higher probabilities of dispersal.

During post-dispersal stages, larger acorns show higher germination rates and produce seedlings more resistant to stressful environmental conditions (Tecklin and McCreary 1991; Gómez 2004; Sage et al. 2011). Thus, on the one hand, producing large seeds may promote seedling recruitment by increasing both the quantity and the quality component of seed dispersal effectiveness (Schupp et al. 2010). On the other hand, larger acorns also entail greater costs per embryo, which may reduce acorn crop (Alejano et al. 2011; Martin et al. 2015). However, the value of food items is context-dependent. In many cases, rodents have to balance between maximizing foraging efficiency and minimizing risks (Lima et al. 1985). For instance, in risky environments like open microhabitats or under bright moonlight (Díaz 1992; Prugh and Golde 2014), rodents tend to minimize seed handling which reduces their discrimination ability, and hence, the influence of seed traits on their harvesting preferences is weaker (Perea et al. 2011; Sunyer et al. 2013). In contrast, when intraspecific competition for seeds is high, rodents invest more effort in safeguarding the most valuable food items from pilferers (Moore et al. 2007; Gálvez et al. 2009), which results in stronger seed trait effects on choice and storage (Pons and Pausas 2007). Thus, whether or not producing more attractive acorns results in enhanced dispersal services is expected to strongly depend on external factors modulating rodents' foraging decisions.

A better understanding of how environmental conditions affect scatter-hoarders' foraging decisions is particularly relevant for oaks. A high proportion of oak woodlands are subjected to anthropogenic disturbances (Santos and Tellería 1998; Dey 2014) that impact risk perception by rodents, per capita acorn availability (Morán-López et al. 2016a, b), as well as seedling recruitment (review in Pulido and Díaz 2005). Therefore, to have a full picture of seed trait effects on successful dispersal, the environmental context in which acorn–rodent encounters occur should be acknowledged. In this work, we use the conditional mutualism among holm oak (*Quercus*

ilex) and the wood mouse (*Apodemus sylvaticus*) as a model system to test the relative importance of seed size and fat content effects on rodents' scatter-hoarding decisions. Holm oak acorns provided us a unique opportunity to test size and fat content effects on mouse preferences using natural seeds instead of artificial ones. There are two subspecies that differ in their fat content but hold similar levels of protein and tannins (Gea-Izquierdo et al. 2006). Additionally, to evaluate how environmental conditions modify seed trait effects, we performed experiments in habitats with contrasting levels of anti-predator cover and rodent abundance—forest sites and small fragments (Morán-López et al. 2015). Labeled acorns of different size (2 vs 5 g) and fat content (3% vs 11%) were offered in forest and small fragments and left for depletion by rodents. With the help of video-recordings, we evaluated acorn trait effects on harvesting preferences, transportation distances, and caching rates.

We expected that seed size would promote dispersal across all stages of the scatter-hoarding process while fat content would mainly affect harvesting time (Wang and Chen 2009; Wang et al. 2013). We also hypothesized that mice would show hierarchical foraging preferences prioritizing seed size over nutrient content (Wang and Chen 2009). Finally, we expected that foraging behaviors aimed at ensuring rapid acquisition of the most valuable food resources (e.g. quick harvesting) would be more important in forest fragments, due to increased competition for acorns (Moore et al. 2007; Sunyer et al. 2013). In contrast, low anti-predator cover in these areas would constrain mouse movements and cache protection strategies resulting in impoverished dispersal services (Morán-López et al. 2015, 2016b).

Materials and methods

Study site and experimental design

Fieldwork was carried out in the northern plateau of the Iberian Peninsula close to the locality of Lerma (42°5′N,3°45′W, 930 m a.s.l.). Landscape is composed of an archipelago holm oak forests located in an extensive treeless agricultural region (Santos and Tellería 1998). The dominant tree is holm oak, with isolated Lusitanian oaks *Q. faginea* and Spanish

junipers *Juniperus thurifera* and understory shrubs typical from wet and cool Supramediterranean localities (e.g. *Cistus laurifolius*, *Genista scorpius*, *Thymus zygis*). Annual precipitation is 567 mm and annual mean temperature 11 °C.

To evaluate the behavioral plasticity of rodents, we selected three plots located in forest sites (> 100 ha) more than 2 km apart and six small forest fragments (0.03 ± 0.01 ha) (Table 4). For each fragmentation category (forest and small fragments), we selected 12 focal trees. Each tree was supplied with a full-factorial design of seeds with contrasting sizes (big and small, 5.00 ± 0.07, 2.37 ± 0.05 g) and fat content (poor and rich, 3 acorns per size–fat content combination, $N = 12$ acorns per tree). Acorns of subsp. *ballota* were considered fat-rich while acorns from the subsp. *ilex* were considered fat poor according to Gea-Izquierdo (2006). To ensure that such classification was correct, we subsequently analyzed the organoleptic composition of acorns from the same source trees as offered ones (see below). Trees located at small fragments show much higher crops than that from forest sites (Morán-López et al. 2016a, b). Overall acorn availability (Moore et al. 2007; Sunyer et al. 2014) and the contrast of traits between environmental acorns and those offered (Lichti et al. 2014) can modify rodents' foraging decisions. Therefore, to test for net size and fat content effects, the experiment was carried in March 2013, outside the acorn fall season (November–January) and when more than 5% of cached acorns have already been recovered (Gómez et al. 2008; Perea et al. 2011b, Morán-López pers. obs.). The timing of the experiment is unlikely to have biased rodents' foraging behavior since previous studies in the area have found similar responses to labeled acorns (e.g., similar overall removal rates) during and outside the acorn fall season (Morán-López et al. 2015).

Experimental acorns were individually marked with a metal wire (Ø 0.6 mm) with a numbered plastic tag attached to it (Xiao et al. 2006a). All acorns were manipulated with gloves to avoid effect of human scent (Duncan et al. 2002). They were placed beneath canopies of focal trees and were protected with $35 \times 35 \times 15$ cm wire cages with 6 cm mesh that only allowed the entrance of rodents. To monitor mouse activity in each focal tree, we installed a video-recording device that consisted on an OmniVision CMOS 380 LTV (3.6 mm lens) camera focused on cages. The system was powered with car batteries and

was fully autonomous for continuous recording during 3 consecutive days (Gallego et al. 2017). Supply points were checked one night after acorn offering.

Fragmentation effects on rodent abundance and anti-predator cover

Rodents were lived-trapped within 3 days of new moon in March 2013 (to control for moonlight effects on reduced rodent activity; Díaz 1992; Perea et al. 2011) by means of Sherman live traps. Forest sites were sampled by means of grids of 6 × 5 traps spaced 10 m, covering an area of 0.3 ha. Small fragments were sampled by means of 1–6 pairs of traps (depending on fragment size, measured on 1:5000 aerial photographs) distributed over the entire fragment. Traps were operated following the standard guidelines of baiting and comfort (Díaz et al. 2010). Trapped mice were identified to species, sexed, and marked (see Morán-López et al. 2015 for details). Complete trapping was corroborated by plotting the number of new recaptures per night against the number of days of exposure. To take into account potential biases in seed trait effects due to rodents' gender (Rosalino et al. 2013), sex ratios of forest fragments were calculated.

Habitat structure was estimated over two 20 m-long, 0.5 m-wide transects established in random directions from each focal tree. Along these transects, we estimated the proportion of open land (bare ground and herbs) and anti-predator cover (shrubs and tree canopies with resprout). Transect length was determined by transportation distances during primary dispersal (< 20 m in most cases) (Gómez et al. 2008, Puerta-Piñero et al. 2010, Morán-López et al. 2015). This way, our estimations of habitat structure were used as a proxy of anti-predator cover availability during acorn transportation from the source point.

Nutritional traits of experimental acorns

In November, we collected for chemical analyses sound and uninfested acorns from 37 to 46 mother trees, *Q. ilex* subsp. *ballota* and subsp. *ilex*, respectively. In each source tree, we collected between 45 and 60 acorns that were subsequently separated in three groups of 15–20 acorns ($N_{ilex} = 1887$; $N_{ballota} = 1930$). Firstly, to ensure that rodents' selectivity was due to fat content and not to differences in acorn

morphology (Muñoz et al. 2012), length and width was measured with digital calipers to the nearest millimeter and a shape parameter (length:width ratio) was calculated. Then, hulls were removed and kernels of acorns from the same group were milled. This flour was dried in a forced-air drier during 48 h at 45 °C. It was then sieved (1-mm mesh) to obtain a fine homogeneous flour. Samples were vacuum-sealed and stored at 4 °C until laboratory analyses (Fernández et al. 2004).

Near-infrared spectroscopy (NIR) was used to translate reflectance spectra of acorns into chemical composition. To take into account potential co-variation among acorn traits, for each source tree we estimated the percentage of crude fat, crude protein, and polyphenols per dry weight. We used polyphenolic compounds as a surrogate of tannins since they constitute the most common polyphenol in acorns (Luczaj et al. 2014). Samples were analyzed at the University of Cordoba NIRS Service (http://www.uco.es/servicios/scai/nir.html). They were scanned using a Foss-NIRSystems 6500 System II spectrophotometer (Foss-NIRSystems Inc., Silver Spring, MD, USA). Reflectance spectra were collected every 2 nm, from 400 to 2500 nm. Data were stored using WinISI II software (Infrasoft International Port Matilda, PA, USA). For translating reflectance values into organoleptic properties, we used the NIR equation developed by Galvan et al. (2012). Samples whose chemical composition was very different from samples used to develop NIR equations (GH > 3) were analyzed in Serida (http://www.serida.org) and "Agroalimentario de Córdoba" laboratories.

Mouse foraging activity

First, we estimated the amount of time mice took to deplete offered acorns upon the first encounter (depletion time hereafter). Then, we evaluated mouse activity during foraging events, which were defined from the entry of an individual into the cage up to its exit. For each foraging event, we measured the duration—to the nearest second—and the proportion of time spent searching for food (moving head down), handling acorns, or vigilant (standing head up) (Hochman and Kotler 2007; Gallego et al. 2017). To evaluate mouse foraging decisions, we divided the scatter-hoarding process into three consecutive events: (1) acorn choice, (2) transportation, and (3) storage. In

each foraging event, we noted which acorn was harvested and whether it was transported outside the cage or not. Transported acorns were searched within a radius of 30 m the day after exposure, and when not found, during the following week. We noted transported distances and whether the handled acorns were cached or not.

Data analysis

Acorn traits and environmental variables

To assess if experimental acorns differed in their chemical content, we used generalized linear models with a binomial response (logit link). Our response variables were proportion of fat, protein, and tannin content (averaged per tree). Our fixed effect was subsp. (*ilex* vs *ballota*). To evaluate if mouse abundance and sex ratios differed between forest sites and small fragments, we used generalized linear models. We modeled the number of mice per 100 traps per night with a Poisson distribution (log link) and the proportion of females with a binomial distribution (logit link). Finally, to test if fragmentation levels showed different anti-predator cover, we used hierarchical binomial models (logit link). Our response variable was the proportion of open land cover (averaged per tree) and our fixed-effect fragmentation level (forest vs small fragment). We introduced site as random factor to take into account spatial autocorrelation of trees located within the same forest sites or within groups of nearby fragments (areas of 35 ha). We fitted all these models using maximum likelihood approximation (lme4 package version 1.0–5., Bates et al. 2011).

Mouse activity

Depletion time was modeled as a Poisson process (log link), which depended on forest fragmentation. Regarding individual events, total event duration (in seconds) was modeled as a Poisson (log link) process, and proportion of time invested on acorn handling and searching were modeled as binomial process (logit link). In all cases, mouse response depended on the fragmentation level (forest, small fragment) and the number of acorns available at the time of the event. In the case of vigilant behaviors, low number of events forced us to use zero-inflated binomial models. The

probability of having a vigilant behavior depended on forest fragmentation, and once this occurred time investment depended on the number of acorns available. In all cases, tree nested in site was introduced as a random factor. See Appendix 1 for model specification.

Mouse scatter-hoarding decisions

To assess acorn choice by rodents, we fitted a hierarchical multinomial model that took into account the number and types (fat content and size) of seeds available in each foraging event. Reference seed trait combination was set to small and fat-rich acorns. Moreover, as rodents may change their selectivity with acorn depletion (Mitchell 1990), we also analyzed the probability of removal during the first or last three foraging events. For this purpose, we used two hierarchical binomial models (logit link), in which our response variables were (1) the first three and (2) the last three acorns removed. In all cases, the probability of removal was modulated by fat content (rich vs poor) and size (small vs big). The strength of these effects depended on fragmentation, which is equivalent to introducing double interactions between fragmentation and acorn traits. Tree nested in site was introduced as a random factor.

To evaluate acorn transportation distances, we used a hierarchical Gaussian model with log-transformed data. The same structure of fixed and random effects as in acorn choice was used. Additionally, we evaluated habitat-type effects on acorn transportation kernels. For this purpose, we estimated skewness, kurtosis, and quantiles of both habitat types using fitdistributionplus package in R (Delignette-Muller et al. 2010). Finally, we analyzed the probability of acorn caching (yes or no) by means of a hierarchical binomial model (logit link). Again, fat content and size modified the probability of storage. The strength of these effects was modulated by fragmentation, and tree nested in site was introduced as a random factor. We fitted models of mouse activity and foraging decisions employing a Bayesian approach with JAGS 3.4.0 (Plumer 2003). For model structure and parameter prior distributions, see Appendix 1. We checked for convergence (Rhat < 1.03) for all model parameters and calculated the mean value of posterior distributions as point estimates and the 95% Highest Posterior Density interval (HPD), also called credible interval,

as a measure of uncertainty around point estimates (Gelman and Hill 2007). In addition, we calculated the proportion of the posterior distribution with the same sign as the mean (f). The effective sample size for each Monte Carlo Markov Chain (MCMC) was always greater than 900. To assess the predictive power of our models, we performed posterior predictive checks (in Appendix 3, Gelman and Hill 2007).

Results

Acorn traits

As expected, main differences in acorn chemical composition were found in fat content. Subsp. *ballota* acorns showed almost four times higher fat content than subsp. *ilex* acorns (10.81 vs 2.80%, respectively; model estimate 1.43 ± 0.11, $P < 0.01$). Acorns from the two subspecies did not differ in protein or tannin content ($P = 0.09$ and $P = 0.33$, respectively, Table 1). Offered acorns had the same shape irrespectively of the population of origin (2.12 ± 0.07, 2.24 ± 0.05, length:width ratio; subsp. *ilex* and subsp. *ballota,* respectively).

Fragmentation effects on rodent abundance and anti-predator cover

All captured rodents were *Apodemus sylvaticus*. Forest fragmentation significantly affected mouse abundance (estimate 1.47 ± 0.36, $P < 0.01$), which was almost four times higher in small fragments than in forest sites (13.00 ± 2.49 vs 3.33 ± 0.64 mice/100 traps per night). However, sex ratios did not differ between habitat types (estimate 0.74 ± 0.83, $P = 0.37$). Regarding anti-predator cover, the proportion of open land around focal trees was greater in small forest fragments (0.62 ± 0.18) than in forest sites (0.28 ± 0.14) (estimate 1.39 ± 0.20, $P < 0.01$).

Mouse activity

Mice harvested 100% of offered seeds during the first night of the experiment. Three cameras failed during the experiment leading to a final sample size of 21 focal trees, 11 of them located in forest sites and 10 of them in forest fragments. We obtained 313 video-recordings out of which 252 corresponded to foraging events. Duration of foraging bouts was similar in both habitats (11.57 ± 0.20 s) and remained unchanged with acorn depletion (Table 2, total time). In general, patterns of time investment in different activities were consistent between habitats. Rodents spent most time in acorn searching and handling while vigilance was a secondary activity (Fig. 1). The amount of time invested in searching and handling did not differ between habitat types though the probability of having a vigilant behavior tended to be higher in forest fragments.

Fragmentation modulated the capacity of rodents to adapt their behavior to acorn availability (Table 2, number of acorn effects). Although average handling times did not differ between habitats (0.44 ± 0.05 and 0.50 ± 0.04 s for forests and fragments, respectively, Table 2); in forest fragments, mice tended to spend more time in acorn handling when all acorns were available. In fact, during the first three foraging bouts, mice spent 29.3% more time in handling activities than in forests. In contrast, in forest sites mice did not adapt their foraging behavior to acorn availability. It only modified time devoted to vigilant behaviors, which represented less than 1% of total time (Table 2).

Mouse scatter-hoarding decisions

The amount of time taken to deplete offered acorns was similar in both types of habitats (48.38 ± 1.52 min on average, mean effect 0.05, $f = 0.50$). Nonetheless, mice foraging decisions differed between habitats. When taking into account all

Table 1 Summary of protein, fat, and tannin content (percentage of dry mass) in acorns of the two subspecies used in our experiment

Subsp	Protein	Fat	Tannin
Q.ilex subsp. *Ilex*	5.44 ± 0.13	2.80 ± 0.39	1.28 ± 0.06
Q.ilex subsp. *ballota*	4.67 ± 0.10	10.81 ± 0.27	1.05 ± 0.04

Values express mean $\pm$ se

Table 2 Summary of mouse activity models

Scatter-hoarding activity	Effect	Habitat type	Mean effect	F	HPD
Total time (s)	Fragmentation	–	0.22	0.80	− 0.91, 1.35
	Number of acorns	Forest	0.00	0.50	− 0.08, 0.08
		Fragment	0.03	0.78	− 0.05, 0.10
Searching (prop.)	Fragmentation	–	0.02	0.57	− 0.98, 1.08
	Number of acorns	Forest	0.00	0.51	− 0.10, 0.10
		Fragment	− 0.05*	0.92	− 0.14, 0.05
Handling (prop.)	Fragmentation	–	− 0.42	0.83	− 1.41, 0.60
	Number of acorns	Forest	− 0.02	0.67	− 0.12, 0.08
		Fragment	**0.09**	**0.96**	**0.00, 0.18**
Vigilance (prop.)	Fragmentation	–	0.93*	0.92	− 0.31, 2.32
	Number of acorns	Forest	− 0.49*	0.90	− 1.34, 0.43
		Fragment	− 0.42*	0.91	− 1.16, 0.37

Mean of posterior distribution (mean effect), percentage of the posterior distribution with the same sign as the mean (f) and highest posterior density interval (HPD). Effects with $f \geq 0.95$ are in bold, effects with $f \geq 0.90 < 0.95$ are marked with *. *Prop* proportion
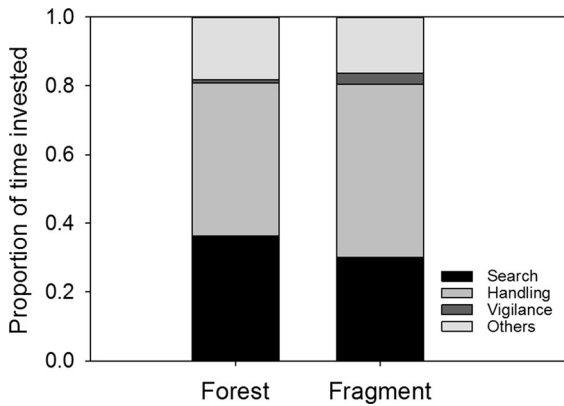

Fig. 1 Proportion of time invested in different activities (handling, searching, and vigilance) in forest habitats and small forest fragments

foraging bouts, acorn choice was driven by size in small fragments (mean effect 1.95, $f = 0.99$; multinomial model) while in forest sites size effects were small (mean effect 0.51, $f = 0.88$). In general, fat content did not affect the overall probability of acorn removal. However, in small forest fragments, within the same seed size category mice tended to preferentially remove fat-rich acorns leading to a late harvesting of small fat-poor ones (Table 3, Fig. 2b).

Maximum and mean transportation distances were similar in both habitat types (22.08 vs 21.53 m; 3.09 vs 4.06 m; forest and fragment sites, respectively). Nonetheless, acorn transportation kernels showed different shapes, with forests showing fatter tails (estimated skewness: 1.61, 2.49, and kurtosis: 4.95, 9.45; forest and fragments, respectively). As a result,

the probability of transportation beyond the canopy of the source tree (> 2 m) was higher in forests (third quantile: 6.47 vs 2.98 m; Fig. 3a). At first glance, acorn traits did not modify transportation distances at forest sites while in small fragments fat-poor acorns were transported further (Fig. 3a, 5.47 ± 0.82 vs 1.91 ± 0.31 m, fat-poor vs fat-rich). However, there was a high variability on fat content effects among source trees leading a non-significant global effect (Table 3). Regarding caching rates, they were higher in forest sites than in small fragments (23.07% vs 13.17% of handled seeds on average). Acorn traits in forest sites did not affect caching rates whereas in small fragments larger acorns had a higher probability of being cached (23% vs 3%, respectively; Table 3, Fig. 3b).

Discussion

Seed encounter by animals represents the first stage of the scatter-hoarding process. During this step, time devoted to different activities will be tightly linked to the effect of acorn traits on the probability of manipulation. In small fragments, where intraspecific competition for seeds was much stronger, rodents adapted their behavior to food availability. When all acorn types were available, they spent more time in acorn handling. This may have helped rodents at gathering information about acorn traits, and hence, at foraging more efficiently by discriminating more valuable food items (Perea et al. 2011; Sunyer et al. 2013). In forest habitats, where competition for seeds

Table 3 Summary of models of the effects of seed traits on scatter-hoarding foraging decisions

Scatter-hoarding decision	Response	Forest type	Factor	Mean effect	F	HPD
Which one to harvest	First to be used	Forest	Size (big)	0.38	0.80	− 0.63, 1.34
			Nut (fat-poor)	− 0.11	0.58	− 1.12, 0.90
		Fragment	**Size (big)**	**0.94**	**0.96**	**− 0.10, 2.01**
			Nut (fat-poor)	− 0.47	0.82	− 1.52, 0.56
	Last to be used	Forest	**Size (big)**	**− 1.64**	**0.97**	**− 3.46, 0.06**
			Nut (fat-poor)	0.40	0.78	− 0.77, 1.56
		Fragment	**Size (big)**	**− 2.24**	**0.99**	**− 4.24, − 0.04**
			Nut (fat-poor)	0.89*	0.93	− 0.35, 2.16
How far transport the seed	Distance	Forest	Size (big)	0.16	0.62	− 1.03, 1.37
			Nut (fat-poor)	0.35	0.70	− 1.12, 1.90
		Fragment	Size (big)	− 0.20	0.64	− 1.35, 0.93
			Nut (fat-poor)	0.58	0.82	− 0.92, 2.02
Consumption or storage	Cached	Forest	Size (big)	0.07	0.53	− 1.91, 2.02
			Nut (fat-poor)	0.76	0.75	− 1.94, 3.37
		Fragment	**Size (big)**	**1.94**	**0.95**	**− 0.58, 4.5**
			Nut (fat-poor)	− 0.32	0.60	− 3.34, 2.53

Mean of posterior distribution (mean effect), percentage of the posterior distribution with the same sign as the mean (f) and highest posterior density interval (HPD). Effects with $f \geq 0.95$ are in bold, effects with $f \geq 0.90 < 0.95$ are marked with *
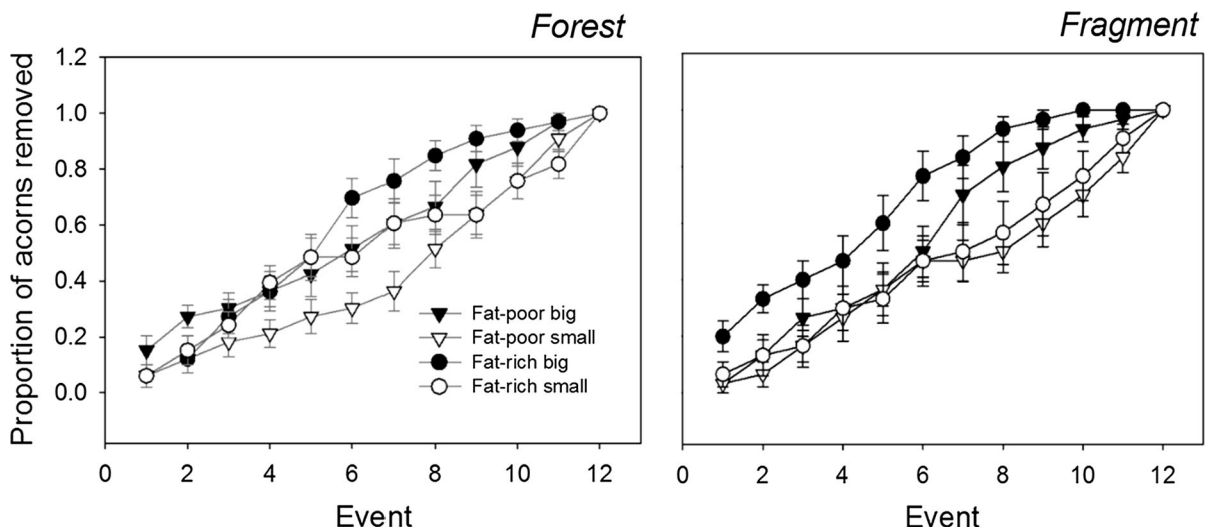

Fig. 2 Effects of acorn size and fat content on time of harvesting in forest sites and small fragments. Values represent mean ± se across focal trees

was much lower, this adaptive behavior disappeared. On one hand, these findings support the idea that in areas with high competition for resources foragers go from a selective behavior to an opportunistic one as food availability decreases, whereas in areas with fewer competitors they mostly behave as generalists (Mitchell 1990, Perea et al. 2011). On the other hand,

they suggest that high intraspecific competition for seeds promotes a more selective harvesting by rodents.

Accordingly, acorn trait effects on mouse scatter-hoarding decisions were stronger in small forest fragments. As found in previous studies, larger acorns were harvested faster (e.g. Perea et al. 2012; Sunyer et al. 2014) and preferentially cached (e.g. Gómez,
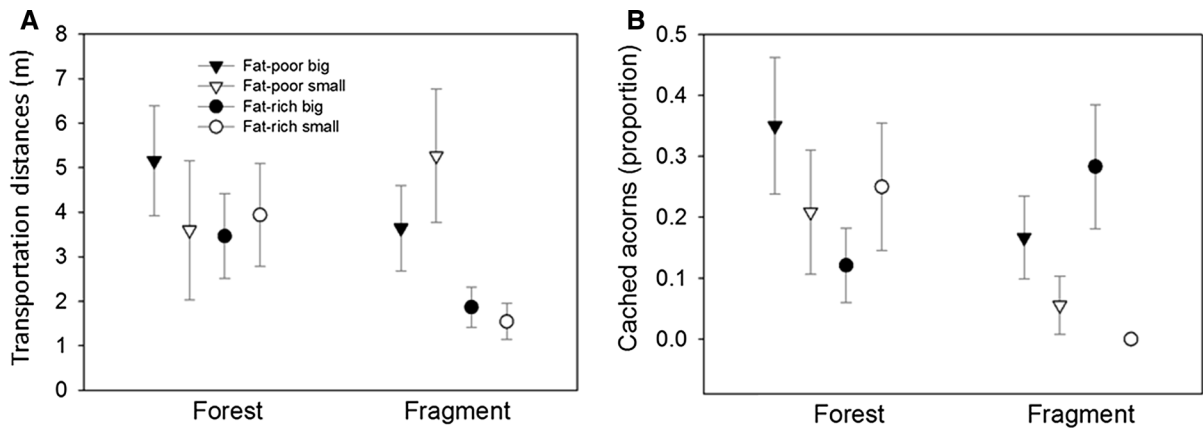
Fig. 3 **a** Size and fat content effects on acorn transportation distances (expressed in m); and **b** caching rates (proportion of handled acorns cached). Values represent mean $\pm$ se across focal trees

et al. 2008; Wang and Chen 2008). Fat content played a secondary role, only enhancing the positive effects of size on seed choice. Thus, our results show that seed size rather than fat content affects the probability of dispersal. This may be because by prioritizing seed size, mice optimize the number of caches to be tracked for the same amount of stored food, since they use size as a proxy of other seed traits (Wang and Chen 2009; Wang et al. 2013; Wang and Yang 2014), or simply because fat content is more cryptic. From the plants' perspective, enhanced dispersal services of larger seeds may imply a double benefit. Larger acorns tend to produce seedlings with higher probabilities to overcome the annual summer drought (Gómez 2004), which is one of the main causes of seedling death in Mediterranean areas (Smit et al. 2008).

Enhanced rodent abundance in fragmented areas has been linked to impoverished dispersal services (Morán-López et al. 2015) and even to regeneration failure due to complete predation of acorn crops (Santos and Telleria 1997). However, preferential caching of "high quality" seeds due to increased intraspecific competition may attenuate such negative impacts, provided that rodents act as moderately efficient acorn dispersers (sensu Gómez et al. 2008). If this was the case, our results suggest that the role of rodents as catalyst of forest regeneration after crop abandonment (Morán-López et al. 2016a, b) could be greater than previously acknowledged. Unfortunately, mowing of surrounding fields precluded us from evaluating seedling emergence and survival. Future studies in fragmented areas surrounded by abandoned

croplands will provide valuable information in this regard.

In contrast to small fragments, in forest sites acorn trait effects were weaker or null. They did not affect the overall probability of removal and only size was negatively linked to late harvesting. Most importantly, seed traits did not affect caching rates. Low intraspecific competition for seeds may have discouraged rodents to forage efficiently (Sunyer et al. 2013). These results support the idea that food value, and hence, the relative importance of seed trait effects on successful dispersal are context-dependent (Lichti et al. 2017). Certain environmental conditions should be met so that rodents forage selectively, and as a result, specific traits affect seed fate. Otherwise, producing expensive seeds may make no difference on the probability of dispersal, an essential initial step for recruitment.

It is important to note, however, that even though rodents were less responsive to acorn traits in forest sites, they provided enhanced dispersal services to oaks. For instance, caching rates were 75% higher. In small fragments, rodents behaved selectively in all stages of the scatter-hoarding process except for transportation. This suggests that environmental conditions in these areas constrain the ability of rodents to carry and cache the most valuable acorns far from tree canopies, where pilferage risks are high. Most probably, lack of anti-predator cover triggered risks during transportation leading to higher acorn predation rates (see Morán-López et al. 2015 for similar results in the study area). Overall, our results point out that when

environmental conditions constrain cache protection strategies, a more selective foraging behavior may not necessarily imply enhanced dispersal services. Besides, they support the idea that high proportion of open land cover is the main environmental factor limiting acorn dispersal in fragmented areas (Morán-López et al. 2015, 2016b).

Conclusions

In general, our results confirm that seed size is a major driver of scatter-hoarders' foraging decisions while fat content plays a secondary role. Moreover, they show that seed trait effects on successful dispersal are context-dependent. Only in forest fragments, where rodents were forced to forage more efficiently due to increased intraspecific competition for seeds, size promoted rapid harvesting and enhanced caching rates. Although this behavior may mitigate the negative impacts of fragmentation on oak regeneration, caching rates were much lower than in forest sites. This suggests that when landscape traits (e.g., high proportions of open land) limit scatter-hoarders' caching strategies, a more selective foraging behavior does not warrant enhanced seed dispersal services for oaks.

Appendix 1: Model structure and priors for every response variable

Total foraging time

We modeled the total foraging time invested by mice as a Poisson process that depended on the fragmentation level (forest or fragment) and the number of acorns available. As acorns were in trees located within sites, we introduced tree nested in site as random factors.

$$y_{i,j,k} \sim \text{Poisson } (\lambda_{i,j,k})$$

$$\log(\lambda_{i,j,k}) = b0_{j,k} + b1 \times \text{fragmentation}_i + b2_{j,k} \\ \times \text{ number of acorns}_i$$

Prior distributions—parameters at tree level

$$b0_{j,k} \sim \text{normal } \left(\mu_k^{b0}, \sigma^{b0}\right)$$

$$b1 \sim \text{normal } (0, 100)$$

$$b2_{j,k} \sim \text{normal } \left(\mu_k^{b2}, \sigma^{b2}\right)$$

Hyper-prior distributions—parameters at site level

$$\mu_k^{b0} \sim \text{normal } \left(\mu^{s0}, \sigma^{s0}\right)$$

$$\mu_k^{b2} \sim \text{normal } \left(\mu_k^{s2}, \sigma^{s2}\right)$$

$$\mu_k^{s2} = \alpha + \delta \times \text{fragmentation}_k$$

$$\sigma^{b0} \sim \text{uniform } (0, 100)$$

$$\sigma^{b2} \sim \text{uniform } (0, 100)$$

$$\mu^{s0} \sim \text{normal } (0, 100)$$

$$\sigma^{s0} \sim \text{uniform } (0, 100)$$

$$\sigma^{s2} \sim \text{uniform } (0, 100)$$

$$\alpha \sim \text{normal } (0, 100)$$

$$\delta \sim \text{normal } (0, 100)$$

$y_{i,j,k}$ is the total foraging time of event i at tree j in site k. $b0$ is the mean time invested in non-fragmented sites, $b1$ depicts fragmentation effects. $b2$ represents the effect of the number of acorns available, which depends on forest fragmentation (α and δ). Each focal tree had a mean $b0$ and $b2$ effect ($b0_{j,k}, b2_{j,k}$), centered on the site where the tree is located μ_k^{b0}, μ_k^{b2}.

Handling—searching time

We modeled proportion of time invested in handling or searching as a binomial process that depended on the fragmentation level (forest or fragment) and the

number of acorns available. As acorns were in trees located within sites, we introduced tree nested in site as random factors.

$$y_{i,j,k} \sim \text{Binomial}\ (p_{i,j,k}, N_i)$$

$$\log \text{it}(p_{i,j,k}) = b0_{j,k} + b1 \times \text{fragmentation}_k + b2_{j,k} \\ \times \text{number of acorns}_i$$

Prior distributions—parameters at tree level

$$b0_{j,k} \sim \text{normal}\ \ (\mu_k^{b0}, \sigma^{b0})$$

$$b1 \sim \text{normal}\ \ (0, 100)$$

$$b2_{j,k} \sim \text{normal}\ \ (\mu_k^{b2}, \sigma^{b2})$$

Hyper-prior distributions—parameters at site level

$$\mu_k^{b0} \sim \text{normal}\ (\mu^{s0}, \sigma^{s0})$$

$$\mu_k^{b2} \sim \text{normal}(\mu_k^{s2}, \sigma^{s2})$$

$$\mu_k^{s2} = \alpha + \delta \times \text{fragmentation}_k$$

$$\sigma^{b0} \sim \text{uniform}\ \ (0, 100)$$

$$\sigma^{b2} \sim \text{uniform}\ \ (0, 100)$$

$$\mu^{s0} \sim \text{normal}\ \ (0, 100)$$

$$\sigma^{s0} \sim \text{uniform}\ \ (0, 100)$$

$$\sigma^{s2} \sim \text{uniform}\ \ (0, 100)$$

$$\alpha \sim \text{normal}\ \ (0, 100)$$

$$\delta \sim \text{normal}\ \ (0, 100)$$

where $y_{i,j,k}$ is either the searching or the handling time of event i at tree j in site k. Here, N is the total time of the foraging ith event. $b0$ is the mean time invested in non-fragmented sites, $b1$ depicts fragmentation effects. $b2$ represents the effect of the number of acorns available, which depends on forest fragmentation (α and δ). Each focal tree had a mean $b0$ and $b2$ effect $(b0_{j,k}, b2_{j,k})$, centered on the site where the tree is located μ_k^{b0}, μ_k^{b2}.

Vigilance time

We modeled time invested in vigilance as a zero-inflated binomial process that depended on the fragmentation level (forest or forest fragment) and the number of acorns available. As acorns were in trees located within sites, we introduced tree nested in site as random factors.

$$y_{i,j,k} \sim \text{Bernoulli}\ (p1_{i,j,k})$$

$$\log \text{it}(p1_{i,j,k}) = a0_{j,k} + a1 \times \text{fragmentation}_k$$

$$r_{i,j,k} \sim \text{Binomial}\ \ \ (p2_{i,j,k}, N_i)$$

$$\log \text{it}(p2_{i,j,k}) = \chi_i \times b1_{j,k} \times \text{number of acorns}_i$$

Prior distributions—parameters at tree level

$$a0_{j,k} \sim \text{normal}\ \ \ (\mu_k^{a0}, \sigma^{a0})$$

$$a1 \sim \text{normal}\ \ \ (0, 100)$$

$$b1_{j,k} \sim \text{normal}\ \ \ (\mu_k^{b1}, \sigma^{b1})$$

Hyper-prior distributions—parameters at site level

$$\mu_k^{a0} \sim \text{normal}\ \ \ (\mu^{s0}, \sigma^{s0})$$

$$\mu_k^{b1} \sim \text{normal}\ (\mu_k^{s1}, \sigma^{s1})$$

$$\mu_k^{s1} = \alpha + \delta \times \text{fragmentation}_k$$

$$\sigma^{a0} \sim \text{uniform}\ \ \ (0, 100)$$

$$\sigma^{a1} \sim \text{uniform}\ \ \ (0, 100)$$

$$\mu^{s0} \sim \text{normal}\ \ \ (0, 100)$$

$$\sigma^{s0} \sim \text{uniform}\ \ \ (0, 100)$$

$$\sigma^{s1} \sim \text{uniform}\ \ \ (0, 100)$$

$$\alpha \sim \text{normal}\ \ \ (0, 100)$$

$$\delta \sim \text{normal}\ \ \ (0, 100)$$

$y_{i,j,k}$ is whether the mouse invested time in vigilance or not during event i at tree j in site k, and $r_{i,j,k}$ is the time invested in vigilance during event i at tree j in site k. The probability of investing time in vigilance ($p1$) depends on fragmentation level (forest or forest fragment). $a0$ is the mean time invested in non-fragmented sites and $a1$ depicts fragmentation effects. The proportion of time invested in vigilance ($p2$) depends on the number of acorns available. $b2$ represents the effect of the number of acorns available,

which depends on forest fragmentation (α and δ). Each focal tree had a mean $b0$ and $b2$ effect $(a0_{j,k}, b1_{j,k})$, centered on the site where the tree is located μ_k^{bo}, μ_k^{b1}.

Depletion time

We modeled the depletion time (in seconds) as a Poisson process that depended on the fragmentation level (forest or fragment). As acorns were in trees located within sites, we introduced tree nested in site as random factors.

$$y_{j,k} \sim \text{Poisson} \quad (\lambda_{j,k})$$

$$\log(\lambda_{j,k}) = \alpha_{i,k} + \beta \times \text{fragmentation}_j$$

   Prior distributions

$$\beta \sim \text{normal} \ (0, 100)$$

   Hyper-prior distributions—parameters at site level

$$\alpha_k \sim \text{normal} \quad (\mu^\alpha, \sigma^\alpha)$$

$$\mu^\alpha \sim \text{normal} \quad (0, 100)$$

$$\sigma^\alpha \sim \text{uniform} \quad (0, 100)$$

   $y_{j,k}$ is the depletion time at tree j in site k. α is the mean time invested in non-fragmented sites and β depicts fragmentation effects. Each site had a mean α_k.

Multiple choice model

We modeled the probability of an acorn being removed taking into account the number and types (fat content and size) of acorns available in each foraging event. This probability depended on acorns fat content and size. As acorns were in trees located within sites, we introduced tree nested in site as random factors.

$$y_{i,j,k} \sim \text{Multinomial} \ (p_{i,j,k}, 1)$$

$$p_{i,j,k} = \frac{e_{i,j,k}}{\sum_i^{N_{i,j,k}} e_{i,j,k}}$$

$$\log(e_{i,j,k}) = b1_{j,k} + b2_{j,k} \times \text{fat content}_i + b3_{j,k} \times \text{size}_i$$

   Prior distributions—parameters at tree level

$$b1_{j,k} \sim \text{normal} \quad (\mu_k^{b1}, \sigma^{b1})$$

$$b2_{j,k} \sim \text{normal} \quad (\mu_k^{b2}, \sigma^{b2})$$

$$b3_{j,k} \sim \text{normal} \quad (\mu_k^{b3}, \sigma^{b3})$$

   Hyper-prior distributions—parameters at site level

$$\mu_k^{b1} \sim \text{normal} \quad (\mu_k^{s1}, \sigma^{s1})$$

$$\mu_k^{b2} \sim \text{normal} \quad (\mu_k^{s2}, \sigma^{s2})$$

$$\mu_k^{b3} \sim \text{normal} \quad (\mu_k^{s3}, \sigma^{s3})$$

$$\mu_k^{s1} = \alpha1 + \delta1 \times \text{fragmentation}_k$$

$$\mu_k^{s2} = \alpha2 + \delta2 \times \text{fragmentation}_k$$

$$\mu_k^{s3} = \alpha3 + \delta3 \times \text{fragmentation}_k$$

$$\sigma^{b1} \sim \text{uniform} \quad (0, 100)$$

$$\sigma^{b2} \sim \text{uniform} \quad (0, 100)$$

$$\sigma^{b3} \sim \text{uniform} \ (0, 100)$$

$$\sigma^{s1} \sim \text{uniform} \quad (0, 100)$$

$$\sigma^{s2} \sim \text{uniform} \ (0, 100)$$

$$\sigma^{s3} \sim \text{uniform} \ (0, 100)$$

$$\alpha1 \sim \text{normal} \ (0, 100)$$

$$\delta1 \sim \text{normal} \quad (0, 100)$$

$$\alpha2 \sim \text{normal} \ (0, 100)$$

$$\delta2 \sim \text{normal} \quad (0, 100)$$

$$\alpha3 \sim \text{normal} \ (0, 100)$$

$$\delta3 \sim \text{normal} \ (0, 100)$$

   $y_{i,j,k}$ is a binary variable that represents whether the acorn i at tree j in site k was removed (1), or not (0). N represents the number of acorns present in that foraging event at that tree. $b1$ is the probability of being removed given that the acorn is small and has low fat content, $b2$ is the effect of fat content, and $b3$ the effect of size. These effects depended on forest fragmentation (α and δ). Each focal tree had a mean

$b1$, $b2$, and $b3$ effect ($b1_{j,k}$, $b2_{j,k}$, $b3_{j,k}$), centered on the site where the tree was located $\left(mu_k^{b1},\ \mu_k^{b2},\ \mu_k^{b3}\right)$.

First and last acorns removed

We modeled the probability of an acorn being removed first or last as a Bernoulli process that depended on their fat content and size. As acorns were in trees located within sites, we introduced tree nested in site as random factors.

$$y_{i,j,k} \sim \text{Bernoulli}\ (p_{i,j,k})$$

$$\log \text{it}(p_{i,j,k}) = b1_{j,k} + b2_{j,k} \times \text{fat content}_i + b3_{j,k} \times \text{size}_i$$

Prior distributions—parameters at tree level

$$b1_{j,k} \sim \text{normal}\ \left(\mu_k^{b1}, \sigma^{b1}\right)$$

$$b2_{j,k} \sim \text{normal}\ \ \left(\mu_k^{b2}, \sigma^{b2}\right)$$

$$b3_{j,k} \sim \text{normal}\ \left(\mu_k^{b3}, \sigma^{b3}\right)$$

Hyper-prior distributions—parameters at site level

$$\mu_k^{b1} \sim \text{normal}\ \ \left(\mu_k^{s1}, \sigma^{s1}\right)$$

$$\mu_k^{b2} \sim \text{normal}\ \ \left(\mu_k^{s2}, \sigma^{s2}\right)$$

$$\mu_k^{b3} \sim \text{normal}\ \ \left(\mu_k^{s3}, \sigma^{s3}\right)$$

$$\mu_k^{s1} = \alpha1 + \delta1 \times \text{fragmentation}_k$$

$$\mu_k^{s2} = \alpha2 + \delta2 \times \text{fragmentation}_k$$

$$\mu_k^{s3} = \alpha3 + \delta3 \times \text{fragmentation}_k$$

$$\sigma^{b1} \sim \text{uniform}\ \ (0, 100)$$

$$\sigma^{b2} \sim \text{uniform}\ \ \ (0, 100)$$

$$\sigma^{b3} \sim \text{uniform}\ \ (0, 100)$$

$$\sigma^{s1} \sim \text{uniform}\ \ (0, 100)$$

$$\sigma^{s2} \sim \text{uniform}\ \ (0, 100)$$

$$\sigma^{s3} \sim \text{uniform}\ \ (0, 100)$$

$$\alpha1 \sim normal\ \ (0, 100)$$

$$\delta1 \sim \text{normal}\ \ (0, 100)$$

$$\alpha2 \sim \text{normal}\ \ (0, 100)$$

$$\delta2 \sim \text{normal}\ \ (0, 100)$$

$$\alpha3 \sim \text{normal}\ \ (0, 100)$$

$$\delta3 \sim \text{normal}\ \ (0, 100)$$

$y_{i,j,k}$ is a binary variable that represents whether the acorn i at tree j in site k was removed first/last (1), or not (0). $b1$ is the probability of being removed first or last given that the acorn is small and has low fat content, $b2$ the effect of fat content, and $b3$ the effect of size. These effects depended on forest fragmentation (α and δ). Each focal tree had a mean $b1$, $b2$, and $b3$ effect ($b1_{j,k}$, $b2_{j,k}$, $b3_{j,k}$), centered on the site where the tree was located $\mu_k^{b1},\ \mu_k^{b2},\ \mu_k^{b3}$.

Dispersal distance

We modeled how far the mice transported the acorns with a normal distribution. We used a logarithmic transformation in other to meet normality. Dispersal distances depended on acorns fat content and size. As acorns were in trees located within sites, we introduced tree nested in site as random factors.

$$\log(y_{i,j,k}) \sim \text{normal}\ (\mu_{i,j,k}, \sigma)$$

$$\mu_{i,j,k} = b1_{j,k} + b2_{j,k} \times \text{fat content}_i + b3_{j,k} \times \text{size}_i$$

Prior distributions—parameters at tree level

$$b1_{j,k} \sim \text{normal}\ \ \left(\mu_k^{b1}, \sigma^{b1}\right)$$

$$b2_{j,k} \sim \text{normal}\ \ \left(\mu_k^{b2}, \sigma^{b2}\right)$$

$$b3_{j,k} \sim \text{normal}\ \left(\mu_k^{b3}, \sigma^{b3}\right)$$

Hyper-prior distributions—parameters at site level

$$\mu_k^{b1} \sim \text{normal}\ \ \left(\mu_k^{s1}, \sigma^{s1}\right)$$

$$\mu_k^{b2} \sim \text{normal}\ \ \left(\mu_k^{s2}, \sigma^{s2}\right)$$

$$\mu_k^{b3} \sim \text{normal}\ \ \left(\mu_k^{s3}, \sigma^{s3}\right)$$

$\mu_k^{s1} = \alpha 1 + \delta 1 \times \text{fragmentation}_k$

$\mu_k^{s2} = \alpha 2 + \delta 2 \times \text{fragmentation}_k$

$\mu_k^{s3} = \alpha 3 + \delta 3 \times \text{fragmentation}_k$

$\sigma \sim \text{uniform} \quad (0, 100)$

$\sigma^{b1} \sim \text{uniform} \quad (0, 100)$

$\sigma^{b2} \sim \text{uniform} \quad (0, 100)$

$\sigma^{b3} \sim \text{uniform} \quad (0, 100)$

$\sigma^{s1} \sim \text{uniform} \quad (0, 100)$

$\sigma^{s2} \sim \text{uniform} \quad (0, 100)$

$\sigma^{s3} \sim \text{uniform} \quad (0, 100)$

$\alpha 1 \sim \text{normal} \ (0, 100)$

$\delta 1 \sim \text{normal} \quad (0, 100)$

$\alpha 2 \sim \text{normal} \quad (0, 100)$

$\delta 2 \sim \text{normal} \quad (0, 100)$

$\alpha 3 \sim \text{normal} \quad (0, 100)$

$\delta 3 \sim \text{normal} \quad (0, 100)$

$y_{i,j,k}$ is the distance acorn i at tree j in site k was dispersed. $b1$ is the mean distance mice transport seeds given they are small and have low fat content, $b2$ the effect of fat content, and $b3$ the effect of size. These effects depended on forest fragmentation (α and δ). Each focal tree had a mean $b1$, $b2$, and $b3$ effect ($b1_{j,k}, b2_{j,k}, b3_{j,k}$), centered on the site where the tree was located μ_k^{b1}, μ_k^{b2}, μ_k^{b3}.

Cached

We modeled if mice consumed or stored the acorns as a Bernoulli process that depended on acorn fat content and size. As acorns were in trees located within sites, we introduced tree nested in site as random factors.

$y_{i,j,k} \sim \text{Bernoulli} \quad (p_{i,j,k})$

$\text{logit}(p_{i,j,k}) = b1_{j,k} + b2_{j,k} \times \text{fat content}_i + b3_{j,k} \times \text{size}_i$

Prior distributions—parameters at tree level

$b1_{j,k} \sim \text{normal} \quad (\mu_k^{b1}, \sigma^{b1})$

$b2_{j,k} \sim \text{normal} \quad (\mu_k^{b2}, \sigma^{b2})$

$b3_{j,k} \sim \text{normal} \quad (\mu_k^{b3}, \sigma^{b3})$

Hyper-prior distributions—parameters at site level

$\mu_k^{b1} \sim \text{normal} \quad (\mu_k^{s1}, \sigma^{s1})$

$\mu_k^{b2} \sim \text{normal} \quad (\mu_k^{s2}, \sigma^{s2})$

$\mu_k^{b3} \sim \text{normal} \quad (\mu_k^{s3}, \sigma^{s3})$

$\mu_k^{s1} = \alpha 1 + \delta 1 \times \text{fragmentation}_k$

$\mu_k^{s2} = \alpha 2 + \delta 2 \times \text{fragmentation}_k$

$\mu_k^{s3} = \alpha 3 + \delta 3 \times \text{fragmentation}_k$

$\sigma^{b1} \sim \text{uniform} \quad (0, 100)$

$\sigma^{b2} \sim \text{uniform} \quad (0, 100)$

$\sigma^{b3} \sim \text{uniform} \quad (0, 100)$

$\sigma^{s1} \sim \text{uniform} \ (0, 100)$

$\sigma^{s2} \sim \text{uniform} \quad (0, 100)$

$\sigma^{s3} \sim \text{uniform} \quad (0, 100)$

$\alpha 1 \sim \text{normal} \quad (0, 100)$

$\delta 1 \sim \text{normal} \quad (0, 100)$

$\alpha 2 \sim \text{normal} \quad (0, 100)$

$\delta 2 \sim \text{normal} \quad (0, 100)$

$\alpha 3 \sim \text{normal} \quad (0, 100)$

$\delta 3 \sim \text{normal} \quad (0, 100)$

$y_{i,j,k}$ is a binary variable that represents whether the acorn i at tree j in site k was cached (1), or not (0). $b1$ is the probability of being cached given that the acorn is small and has low fat content, $b2$ the effect of fat

content and $b3$ the effect of size. These effects depended on forest fragmentation (α and δ). Each focal tree had a mean $b1$, $b2$, and $b3$ effect ($b1_{j,k}, b2_{j,k}, b3_{j,k}$), centered on the site where the tree was located μ_k^{b1}, μ_k^{b2}, μ_k^{b3}.

Appendix 2

See Table 4.

Table 4 Location and area of forest fragments used in the study

Fragment	Category	Latitude (N)	Longitude (w)	Area (ha)
p12	Small fragment	41°59′1.34″	3°46′54.20″	0.020
p14	Small fragment	41°58′58.64″	3°47′22.30″	0.029
p15	Small fragment	41°59′3.03″	3°47′21.65″	0.049
p16	Small fragment	41°59′17.73″	3°47′5.78″	0.040
p18	Small fragment	41°59′20.28″	3°47′29.76″	0.036
p22	Small fragment	41°58′7.77″	3°48′9.69″	0.012
G1	Forest site	42° 1′29.54″	3°50′18.71″	2773.672
G2	Forest site	41°58′22.91″	3°47′12.73″	296.379
G3	Forest site	42° 1′04.19″	3°49′26.78″	2773.672

Appendix 3 Posterior predictive checks of Bayesian models

Mouse foraging activity

See Figs. 4, 5, 6, and 7.
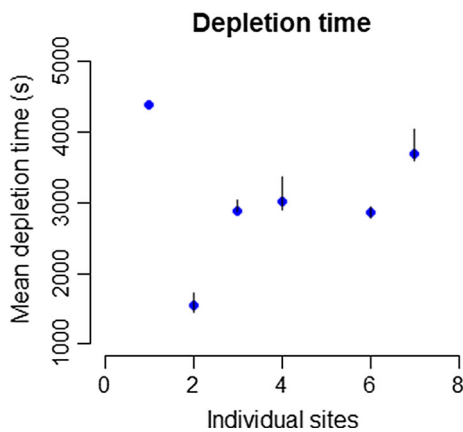
Fig. 4 Posterior predictive check of models of fragmentation effects on depletion time. Blue dots represent mean values of data; bars represent credible intervals of model predictions
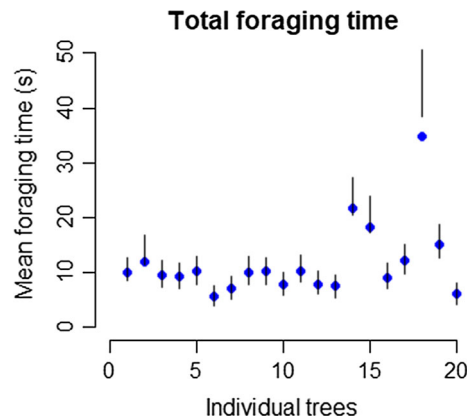

Fig. 5 Posterior predictive check of models of fragmentation effects on total foraging time. Blue dots represent mean values of data; bars represent credible intervals of model predictions
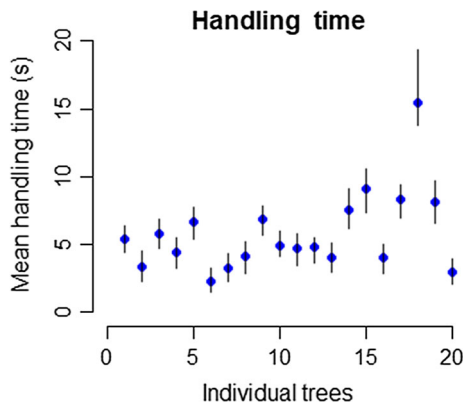
Fig. 6 Posterior predictive check of models of fragmentation effects on proportion of time invested in acorn handling. Blue dots represent mean values of data; bars represent credible intervals of model predictions
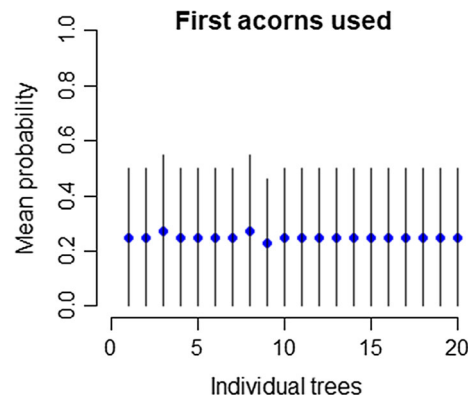

Fig. 8 Posterior predictive check of models of the probability of an acorn being removed during the first three foraging bouts. Blue dots represent mean values of data; bars represent credible intervals of model predictions
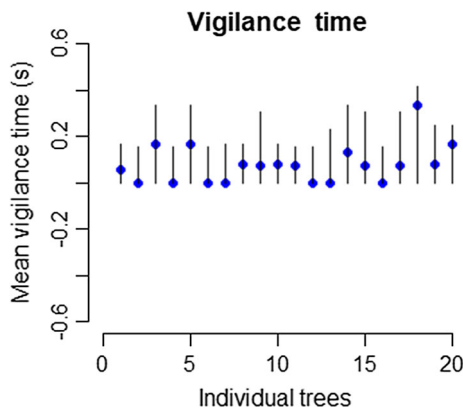

Fig. 7 Posterior predictive check of models of fragmentation effects on proportion of time invested in vigilant behaviors. Blue dots represent mean values of data; bars represent credible intervals of model predictions
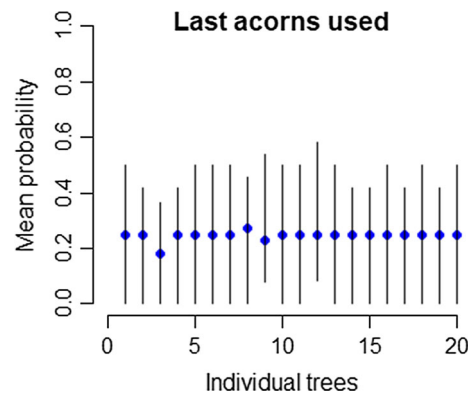
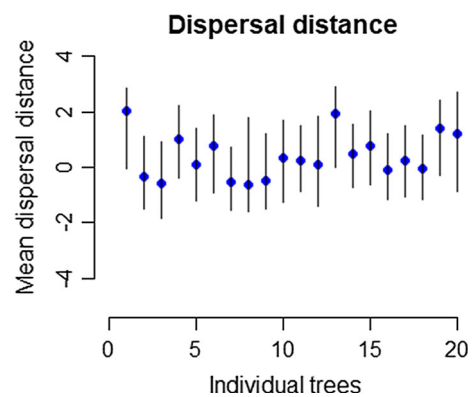Mouse foraging decisions

See Figs. 8, 9, 10, and 11.

Fig. 9 Posterior predictive check of models of the probability of an acorn being removed during the first three foraging bouts. Blue dots represent mean values of data; bars represent credible intervals of model predictions

Fig. 10 Posterior predictive check of models of acorn transportation distances. Blue dots represent mean values of data; bars represent credible intervals of model predictions
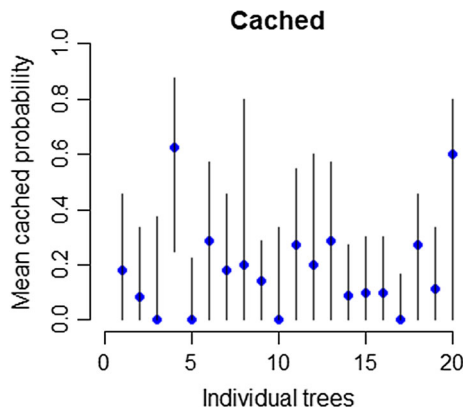
Fig. 11 Posterior predictive check of models of the probability of an acorn being cached. Blue dots represent mean values of data; bars represent credible intervals of model predictions

References

Alejano R, Vazquez-Pique J, Carevic F, Fernandez M (2011) Do ecological and silvicultural factors influence acorn mass in Holm Oak (southwestern Spain)? Agroforest Syst 83:25–39

Bates D, Maechler M, Bolker B, Walker S (2011) lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0–5

Delignette-Muller ML, Pouillot R, Denis JB, Dutang C (2010) Fitdistrplus: help to fit of a parametric distribution to non-censored or censored data

Dey DC (2014) Sustaining oak forests in Eastern North America: regeneration and recruitment, the pillars of sustainability. For Sci 60:926–942

Díaz M (1992) Rodent seed predation in cereal crop areas of central Spain—Effects of physiognomy, food availability, and predation risk. Ecography 15:77–85

Díaz M, Torre I, Arrizabalaga A (2010) Relative roles of density and rainfall on the short-term regulation of Mediterranean wood mouse *Apodemus sylvaticus* populations. Acta Theriol 55:251–260

Duncan RS, Wenny DG, Spritzer MD, Whelan CJ (2002) Does human scent bias seed removal studies? Ecology 83:2630–2636

Fernández I, Gómez A, Moreno P et al (2004) Variabilidad de las características de las bellotas en el Valle de los Pedroches (Córdoba). *Pastos y Ganadería Extensiva; XLIV Reunión Científica de la SEEP* (ed. G.C.A. García Criado B., Vázquez de Aldana, B.R.., Zabalgogeazcoa I.), pp. 317–322. SEEP

Gallego D, Morán-López T, Torre I, Navarro-Castilla A, Barja I, Díaz M (2017) Context dependence of acorn handling by the Algerian mouse (*Mus spretus*). Acta Oecol 84:1–7

Galvan JV, Jorrin Novo JJ, Gómez-Cabrera A, Ariza D, García-Olmo J, Navarro Cerrillo RM (2012) Population variability based on the morphometry and chemical composition of the acorn in Holm oak (*Quercus ilex* subsp. *ballota* Desf. Samp.). Eur J For Res 131:893–904

Gálvez D, Kranstauber B, Kays RW, Jansen PA (2009) Scatter hoarding by the Central American agouti: a test of optimal cache spacing theory. Anim Behav 78:1327–1333

Gea-Izquierdo G, Cañellas I, Montero G (2006) Acorn production in Spanish holm oak woodlands. Invest. Agrar 15:339–354

Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge

Gómez JM (2004) Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. Evolution 58:71–80

Gómez JM, Puerta-Pinero C, Schupp EW (2008) Effectiveness of rodents as local seed dispersers of Holm oaks. Oecologia 155:529–537

Hochman V, Kotler BP (2007) Patch use, apprehension, and vigilance behavior of Nubian Ibex under perceived risk of predation. Behav Ecol 18:368–374

Jansen PA, Bongers F, Hemerik L (2004) Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. Ecol Monogr 74:569–589

Lichti NI, Steele MA, Zhang H, Swihart RK (2014) Mast species composition alters seed fate in North American rodent-dispersed hardwoods. Ecology 95:1746–1758

Lichti NI, Steele MA, Swihart RK (2017) Seed fate and decision-making processes in scatter-hoarding rodents. Biol Rev 92:474–504

Lima SL, Valone TJ, Caraco T (1985) Foraging-efficiency-predation-risk trade-off in the grey squirrel. Anim Behav 33:155–165

Luczaj L, Adamczak A, Duda M (2014) Tannin content in acorns (*Quercus* spp.) from Poland. Dendrobiology 72:103–111

Martín D, Vázquez-Piqué J, Carevic F, Fernández M, Alejano R (2015) Trade-off between stem growth and acorn production in holm oak. Trees 29:825–834

Mitchell WA (1990) An optimal-control theory of diet selection—the effects of resource depletion and exploitative competition. Oikos 58:16–24

Moore JE, McEuen AB, Swihart RK, Contreras TA, Steele MA (2007) Determinants of seed removal distance by scatter-hoarding rodents in deciduous forests. Ecology 88:2529–2540

Morán-López T, Fernández M, Alonso CL, Flores-Rentería D, Valladares F, Diaz M (2015) Effects of forest fragmentation on the oak–rodent mutualism. Oikos 124:1482–1491

Morán-López T, Forner A, Flores-Rentería D, Díaz M, Valladares F (2016a) Some positive effects of the fragmentation of holm oak forests: attenuation of water stress and enhancement of acorn production. Forest Ecol Manag 370:22–30

Morán-López T, Wiegand T, Morales JM, Valladares F, Díaz M (2016b) Predicting forest management effects on oak–rodent mutualisms. Oikos 125:1445–1457

Muñoz A, Bonal R, Espelta JM (2012) Responses of a scatter-hoarding rodent to seed morphology: links between seed choices and seed variability. Anim Behav 84:1435–1442

Perea R, Gonzalez R, San Miguel A, Gil L (2011) Moonlight and shelter cause differential seed selection and removal by rodents. Anim Behav 82:717–723

Perea R, Miguel AS, Martinez-Jauregui M, Valbuena-Carabana M, Gil L (2012) Effects of seed quality and seed location on the removal of acorns and beechnuts. Eur J For Res 131:623–631

Pérez-Ramos IM, Urbieta IR, Maranon T, Zavala MA, Kobe RK (2008) Seed removal in two coexisting oak species: ecological consequences of seed size, plant cover and seed-drop timing. Oikos 117:1386–1396

Pesendorfer MB, Sillett TS, Koenig WD, Morrison SA (2016) Scatter-hoarding corvids as seed dispersers for oaks and pines: a review of a widely distributed mutualism and its utility to habitat restoration. Condor 118:215–237

Plumer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling URL http://citeseer.ist.psu.edu/plummer03jags.html

Pons J, Pausas JG (2007) Rodent acorn selection in a Mediterranean oak landscape. Ecol Res 22:535–541

Prugh LR, Golde CG (2014) Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. J Anim Ecol 83:504–514

Puerta-Piñero C, Gómez JM, Schupp FW (2010) Spatial patterns of acorn dispersal by rodents: do acorn crop size and ungulate presence matter? Oikos 119:179–187

Pulido FJ, Díaz M (2005) Regeneration of a Mediterranean oak: a whole-cycle approach. EcoScience 12:92–102

Rosalino LM, Nobrega F, Santos-Reis M, Teixeira G, Rebelo R (2013) Acorn selection by the wood mouse Apodemus sylvaticus: a semi-controlled experiment in a mediterranean environment. Zool Sci 30(9):724–730

Sage RD, Koenig WD, McLaughlin BC (2011) Fitness consequences of seed size in the valley oak Quercus lobata N, e (Fagaceae). Ann For Sci 68(3):477–484

Santos T, Telleria JL (1997) Vertebrate predation on Holm Oak, Quercus ilex, acorns in a fragmented habitat: effects on seedling recruitment. For Ecol Manag 98(2):181–187

Santos T, Tellería JL (1998) Efectos de la fragmentación de los bosques sobre los vertebrados de las mesetas ibéricas. Organismo Autónomo "Parques Nacionales," Madrid, Spain

Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: a conceptual review. New Phytol 188(2):333–353

Smit C, den Ouden J, Díaz M (2008) Facilitation of Quercus ilex recruitment by shrubs in Mediterranean open woodlands. J Veg Sci 19(2):193–200

Sunyer P, Muñoz A, Bonal R, Espelta JM (2013) The ecology of seed dispersal by small rodents: a role for predator and conspecific scents. Funct Ecol 27:1313–1321

Sunyer P, Espelta JM, Bonal R, Muñoz A (2014) Seeding phenology influences wood mouse seed choices: the overlooked role of timing in the foraging decisions by seed-dispersing rodents? Behav Ecol Sociobiol 68:1205–1213

Tecklin J, McCreary DD (1991) Acorn size as a factor in early seedling growth of blue oaks. In: Proceedings of the symposium on oak woodlands and hardwood rangeland management. October 31–November 2, 1990; Davis, California. Gen. Tech. Rep. PSW-GTR-126. Berkeley, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; p. 48–53

Vander Wall SB (1990) Food Hoarding in Animals. University Chicago Press, Chicago

Vander Wall SB (2001) The evolutionary ecology of nut dispersal. Bot Rev 67:74–117

Wang B, Chen J (2008) Tannin concentration enhances seed caching by scatter-hoarding rodents: an experiment using artificial 'seeds'. Acta Oecol 34:379–385

Wang B, Chen J (2009) Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. Ecology 90:3023–3032

Wang B, Chen J (2012) Effects of fat and protein levels on foraging preferences of tannin in scatter-hoarding rodents. PLoS ONE 7:e40640

Wang B, Yang XL (2014) Teasing apart the effects of seed size and energy content on rodent scatter-hoarding behavior. PLoS ONE 9:e111389

Wang B, Ye CX, Cannon CH, Chen J (2013) Dissecting the decision making process of scatter-hoarding rodents. Oikos 122:1027–1034

Xiao ZS, Jansen PA, Zhang ZB (2006a) Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. Forest Ecol Manag 223:18–23

Xiao ZS, Wang YS, Harris M, Zhang ZB (2006b) Spatial and temporal variation of seed predation and removal of sympatric large-seeded species in relation to innate seed traits in a subtropical forest Southwest China. Forest Ecol Manag 222:46–54