



Context dependence of acorn handling by the Algerian mouse (*Mus spretus*)



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ABSTRACT

Perceived predation risk and competition for acorns are expected to affect scatter-hoarding decisions by Algerian mice (*Mus spretus*). We manipulated both factors by means of predator fecal scents and ungulate exclosures. We hypothesized that high-risk perception and ungulate presence would promote acorn dispersal. In the former case, it would stimulate acorn mobilization to safe microhabitats rather than *in situ* consumption. In the latter, increased competition for acorns would promote their storage for later consumption. We also expected that mice would adapt their foraging behavior to previous experience modulating the strength of these effects.

In the presence of ungulates, mice focused their foraging activities on food acquisition at the expenses of vigilant behaviors. However, a more efficient foraging did not entail enhanced dispersal services. Lack of anti-predatory cover in tree surroundings may have deterred mice from transporting seeds outside canopies. Increased risk interacted with previous experience. In control trees (no predator odor), mice confidence increased throughout the night resulting in decreased vigilance and enhanced acorn mobilization rates. In contrast, in risky conditions (trees with predator odor) mice maintained a base-line vigilant behavior. Contrary to our expectations, increased risk did not result in higher acorn mobilization, but the opposite. Again, the scarcity of safe microhabitats for mobilization may have been the underlying cause of this behavior.

Our results show that successful acorn dispersal depends, at least partly, on plant-animal relationships that are beyond the oak-rodent mutualism. Thus, any conservation policy aimed at restoring natural regeneration of oaks should take into account the interaction network in which oak-rodent encounters are embedded. In addition, they suggest that mice incorporate direct and indirect cues of risks (habitat structure) through recent experience. A better understanding of this process will improve our ability to incorporate such temporal and spatial variability in models of acorn dispersal.

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1. Introduction

Natural regeneration of large-seeded, dominant trees in temperate habitats critically depends on the foraging activity of

animals that store seeds for later consumption (Den Ouden et al., 2005; Herrera and Pellmyr, 2009; Vander Wall, 1990). Seed dispersal by scatter-hoarding animals is a classic example of a conditional mutualism (Bronstein, 1994). The interaction will only become mutualistic if seeds are deposited in areas where seedling recruitment can occur and they escape post-dispersal retrieval (Bronstein, 1994; Herrera and Pellmyr, 2009). Such fine balance between predation and dispersal often depends on environmental factors that modulate the costs and benefits of *in situ* consumption vs. transport and hoarding (Lichti et al., 2017). In particular, *per capita* seed availability and predation risks during transportation are key factors to understand the foraging behavior of scatter-

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hoarding rodents (Morán-López et al., 2015b; Perea et al., 2011a; Theimer, 2005).

In general, when *per capita* seed availability is low due to high intra-specific competition, rodents tend to store seeds to ensure rapid acquisition of food and invest more effort in locating caches in areas where pilfering risks are low (Moore et al., 2007; Puerta-Piñero et al., 2010; Morán-López et al., 2016). This results in enhanced mobilization distances and caching rates and, consequently, in increased dispersal services provided to plants (Dally et al., 2006; Morán-López et al., 2016). Effects of inter-specific competition may be less straightforward. For instance, ungulates compete with rodents for acorns (Smit et al., 2008; Muñoz et al., 2009). Hence, their presence is expected to stimulate acorn transport and storage. Nonetheless, they also reduce habitat quality for rodents (Keesing, 1998; Torre et al., 2007; Muñoz et al., 2009; Navarro-Castilla et al., 2017b), which results in lower abundance (Muñoz et al., 2009; Navarro-Castilla et al., 2017b) and relaxed intra-specific competition for seeds. Depending on these two opposing processes, ungulate presence may promote acorn dispersal or not.

Perceived predation risk is the other main factor influencing rodent foraging decisions (Caro, 2005; Lima and Dill, 1990; Morán-López et al., 2016). Rodents rely on both direct and indirect cues to assess predator presence and to behave accordingly (Díaz et al., 2005; Orrock et al., 2004). Indirect cues provide information on general risks related to microhabitat structure (e.g. availability of vegetation cover or refuges - Orrock et al., 2004 - or moonlight - Díaz, 1992). Individuals usually forage in the safer places or times according to these indirect cues (Díaz, 1992; Navarro-Castilla and Barja, 2014b; Perea et al., 2011a, 2011b), but they may also reduce foraging activity in the presence of predators (Díaz et al., 2005). Moreover, predator presence may produce fast dispersal of acorns to safer sites, particularly if their consumption requires substantial handling time (Lichti et al., 2017). Thus, increased risk perception can promote acorn dispersal (Steele et al., 2014).

Although the effects of competition and risk on scatter hoarders' foraging decisions have been well documented (see Lichti et al., 2017 for a review), most studies have focused on "average behavioral patterns" (*sensu* Sunyer et al., 2013) overlooking intra-specific variability. However, the strength of these effects is expected to vary with individual factors (i.e. sex, age) that modulate the balance of costs and benefits of scatter-hoarding (Godsall et al., 2014; Navarro-Castilla and Barja, 2014a). Moreover, under field conditions it would be expected that mice modify their foraging behavior after sequential exposure to predator or competitor signals, eventually modulating the initial effects of these signals (Lönnstedt et al., 2012; Crane and Ferrari, 2013). Assessing how individual mice adapt their responses to environmental factors according to recent experience will improve our understanding of the behavioral mechanisms driving their foraging behavior, and consequently, the dispersal services they provide (Cousens et al., 2010; Morán-López et al., 2016).

Here we used a field experiment designed to evaluate the effects of predation risk, competition and previous experience on individual mice foraging behavior and its effects on acorn dispersal. Predation risk was manipulated by addition of a direct cue, predator scent, whereas competition for acorns was manipulated by means of ungulate exclosures. We expected enhanced acorn dispersal when mice experienced high risk of predation and when ungulates were present. In the former case, due to acorn mobilization to safe sites. In the latter, because increased inter-specific competition for seeds would cancel out the impacts of relaxed intra-specific competition. Finally, we hypothesized that the effects of these environmental factors would be modulated by previous experience.

2. Materials and methods

2.1. Study area and species

Field work was carried out in the savanna-like holm oak *Quercus ilex* woodlands of the Cabañeros National Park (Central Spain; 39 °24'N, 38 °35'W). Holm oaks grow scattered on a grassland matrix with almost no shrub cover (<1%; Díaz et al., 2011; Morán-López et al., 2015a). Tree density around focal trees was 20.4 ha⁻¹ on average (range 1.5–65.5), as measured on aerial photographs. Dehesas (savanna-like holm oak woodlands) suffer from a chronic regeneration failure due to insufficient acorn dispersal to safe sites for oak establishment (Campos et al., 2013; Pulido and Díaz, 2005).

Red deer (*Cervus elaphus*) has densities of 0.14 inds/ha on average in Cabañeros National park (Jiménez, 2004). Wild boars (*Sus scrofa*) are also abundant but without data on densities (Perea and Gil, 2014). The study area covers around 780 ha, including two ungulate exclosures (150 ha and 4.65 ha) separated from each other by 1500 m. Ungulate exclosures consist of 2-m-high fences with a mesh width of 32 cm × 16 cm. They prevent the entrance of ungulates but allow free passage of terrestrial predators (mainly red foxes *Vulpes vulpes*, badgers *Meles meles*, stone martens *Martes foina* and common genet *Genetta genetta*, as verified by scat counts inside and outside exclosures; unpublished data), and raptors. Areas with ungulate exclosures are paired with adjacent non-excluded zones, with a similar size and tree abundance (see Díaz et al., 2011 for a more detailed description). Each combination of exclosure-control treatments will correspond to an experimental site hereafter.

The Algerian mouse is the most abundant scatter-hoarding rodent in the area (Díaz et al., 2011). It is the main disperser of holm oak acorns in open oak woodlands, where the activity of jays *Garrulus glandarius* and wood mice *Apodemus sylvaticus* is low or absent (Morán-López et al., 2015a; Muñoz et al., 2009). Algerian mice are preyed by a wide range of animals including genets (*Genetta genetta*; Palomo et al., 2009; Torre et al., 2013). Common genet presence or presence of genet scent have been proven to modify rodent foraging behavior (Díaz et al., 2005; Navarro-Castilla and Barja, 2014a; Navarro-Castilla et al., 2017a).

2.2. Experimental design

In each experimental site, among the trees known to be occupied by Algerian mice by trapping (see below), we randomly selected 10 trees inside and 10 trees outside the exclosure (N = 2 sites × 2 exclosure treatments × 10 trees = 40). Tree occupancy by mice was established by means of live-trapping (Navarro-Castilla et al., 2017b) using Sherman traps (23 × 7.5 × 9 cm; Sherman Co., USA; Torre et al., 2016). We paired selected trees according to their proximity in space. Then, we assigned a predator odor treatment randomly to one of them to ensure spatial interspersed of treatments and odorless controls (5 with odor, 5 control). Treatment consisted in placing a small amount (10 g) of fresh genet feces mixed with distilled water close to a corner of the acorn cages (see below). Droppings came from captive genets from the 'Cañada Real' Nature Center of Iberian fauna (Madrid, Spain). We performed all manipulations with disposable latex gloves, to avoid human odor (Wenny, 2002).

We installed a 50 cm × 50 cm × 15 cm galvanized-steel cage, close to tree trunks, with a mesh width of 5 cm × 5 cm, to prevent acorn consumption by birds or ungulates (Díaz et al., 2011). In each focal tree, we placed 15 sound acorns taken from holm oaks growing near the study area at the start of the experiment in each cage (N_{acorns} = 40 × 15 = 600). To monitor mice foraging activity, trees were provided with video-cameras OmniVision CMOS 380

LTV (3.6 mm lens) focused on the cages and mounted on a tripod 150 cm tall located 2.5 m away. Video cameras were provided with ELRO dvr32 card-based recorders, and the video recording set was powered by car batteries (70 Ah, acid-lead) attached to solar panels (mono-silicon erial P_20; 20 w). The system was fully autonomous for continuous recording during three consecutive days by setting the recording quality at 5 frames s⁻¹ and using 16 GB recording cards that were replaced daily early in the morning.

2.3. Mouse foraging behavior

We recorded mice foraging behavior during three consecutive full-moon nights in early February 2012. The experiment was carried out in February instead of during the natural acorn fall season (November–January) to equalize background acorn availability among enclosure treatments. Besides, previous studies in Mediterranean areas have observed that rodent responses to experimental acorns are consistent between the acorn fall season and early winter (Morán-López et al., 2015b). We visualized full recordings at high speed to locate foraging events, which were subsequently analyzed individually at normal speed.

Mouse foraging events were defined from the entry of the individual into the cage up to the exit from it. Initially, we attributed all the events in each tree to one individual (dominant, the owner of the territory). Nevertheless, video recordings showed that some trees were occupied by more than one individual. Based on video data, dominant individuals were identified by their larger size (as established for comparison with the wire mesh size) and their territorial behavior (Hurst et al., 1996). We focused the analyses of behavioral responses of dominant individuals.

For all foraging events, we noted the number of previous visits per night by the focal dominant individual. We measured the duration of events to the nearest second on video records, as well as the proportion of time spent searching for food (moving head down), handling acorns, or vigilant (standing head up) (Hochman and Kotler, 2007). Finally, to link foraging behavior with acorn mobilization rates we noted whether individuals took the handled acorn out from the cage or not.

2.4. Environmental factors

Ungulate enclosure has led to higher herb cover among scattered trees and higher resprout development under trees (Muñoz et al., 2009; Navarro-Castilla et al., 2017b). In order to take into account potential biases due to changes in vegetation cover, in each focal tree we estimated the extension and height of resprouts. Extension was estimated from the mean of N-S and E-W diameters measured to the nearest cm with a tape, assuming a roughly circular shape. Mean height of the resprout patches was measured to the nearest cm with a ruler put vertically on the ground 10 times per patch. Ruler positions were spaced regularly along transects surrounding tree trunks (Newton, 2007). Since our video recording showed the presence of non-dominant mice that tried to forage on cages, we counted the number of previous visits of intruders as a proxy of intra-specific competition for seeds.

2.5. Data analysis

To rule out that differences between treatments were due to changes in tree resprout cover we performed preliminary regression analyses. Response variables were tree resprout area (m²) and height (cm), and fixed effects were ungulate presence, scent exposure and their interaction. In addition, we evaluated if intra-specific competition differed among treatments. For this purpose, we used generalized linear models (log link). Our response variable

was number of visits of intruders throughout the night. Our fixed effects were ungulate presence, scent exposure and their interaction (Table A1).

To assess the effects of ungulate presence and risk perception on mouse foraging decisions we used generalized mixed models. Response variables were event duration (in seconds) and proportion of time spent vigilant and acorn manipulation. Fixed effects were ungulate presence (yes/no), scent treatment (yes/no), number of previous visits to the focal tree (counts) and their two-way interactions. Model selection was performed according to the Akaike information criterion ($|\Delta AIC| > 2$, Burnham and Anderson, 2010). Tree nested in night was included as a random factor in the intercept to account for statistical dependence of records from the same individual. We used Poisson (log link) function for event duration and binomial (logit link) for the rest of variables. Trees were considered as independent within experimental sites since minimum distances between focal trees ranged between 18.36 and 90.62 m. These values are beyond average home-range radius reported for *Mus spretus* (10.45 m; Díaz et al., 2011; Gray et al., 1998). Variogram tests on model residuals (not shown) confirmed this initial assumption (R package gstat; Pebesma, 2004).

To test if the probability of taking an acorn out of the cage depended on risk perception and its interaction with ungulate presence we used generalized binomial mixed models. The response variable was acorn transportation (1: carried outside the cage, 0: consumed *in situ*) and the explanatory variables were proportion of time spent vigilant and its interaction with ungulate presence (yes/no). Tree nested in night was introduced as a random factor. For these analyses we used Lme4 package (Bates et al., 2015).

High number of events without any previous visit of intruders precluded us from performing regression analyses to test for intra-specific competition effects. Instead, we performed Spearman's correlation analysis between number of previous visits by intruders and event duration, vigilance and manipulation. Correlation analyses were performed pooling all data together as well as separating them by ungulate presence and scent exposure treatments.

3. Results

Resprout cover and height in occupied trees was similar inside and outside enclosures (9.9 ± 2.7 vs 10.5 ± 2.9 m² and 82.3 ± 11.3 cm vs 52.3 ± 12.0 ; Table A1). Out of the 40 focal trees initially attempted in our experimental design, our final sample size was of 25 trees. Fourteen trees recorded no activity and one tree was occupied by a wood mouse *Apodemus sylvaticus*. Overall, we obtained 1236 events of mice searching and/or manipulating acorns inside cages, out of which 987 were from dominant individuals.

On average, each dominant individual performed 47.0 (± 8.9) foraging events and the number of foraging events did not differ between treatments ($P = 0.19$ and $P = 0.69$, for scent and ungulate presence effects, respectively). Mean duration of foraging bouts was higher in the presence of ungulates (62.2 ± 0.3 vs 55.3 ± 0.4 s), and these effects became stronger throughout the night (Table 1, Ungulates x Visits). However, in this model fixed effects only accounted for 3% of the total variance, and most variance in event duration was due to random (individual) effects. Regarding time budgets, previous experience reduced time spent in acorn handling, but these effects were weaker when ungulates were present (Table 1). Scent treatment had no net or interactive effect. Again, fixed effects only accounted for a 6% of the total variance whereas most variance was due to random (individual) effects. In contrast, when assessing vigilant behaviors fixed effects accounted for 45% of the variance explained by the model ($R^2_m = 0.11$, $R^2_c = 0.24$). In general, mice spent less time vigilant when ungulates were present (Table 1, Fig. 1A). Scent treatment had no net

Table 1
Summary of optimal generalized mixed models with mouse foraging behavior as a function of ungulate presence (yes, no), scent exposure (yes, no), previous visits during the night (visits) and their double interactions. Response variables were event duration (in seconds), and proportion of time spent vigilant and acorn handling. Boldface indicates significant results. LRT = likelihood ratio test, *d.f.* = degrees of freedom, *b* = slope estimate, R^2_m = marginal pseudo R^2 (proportion of variance explained by fixed effects), R^2_c = conditional pseudo R^2 (overall variance explained). Baselines-ungulate absence and no genet scent treatment.

Response	Fixed effect	LRT	<i>d.f.</i>	P	<i>b</i>	SE (<i>b</i>)	R^2_m	R^2_c
Event duration	Ungulates	7.00	1	0.01	0.20	0.18	0.03	0.19
	Visits	1.63	1	0.20	−0.03	0.01		
	Ungulates x Visits	5.06	1	0.02	0.03	0.01		
Vigilance	Ungulates	16.08	1	<0.001	−1.54	0.38	0.11	0.24
	Scent	0.03	1	0.86	−0.18	0.41		
	Visits	93.35	1	<0.001	−0.02	0.00		
	Scent x Visits	45.64	1	<0.001	0.04	0.01		
Acorn handling	Ungulates	5.10	1	0.84	0.57	0.85	0.06	0.24
	Visits	45.07	1	<0.001	−0.08	0.00		
	Ungulates x Visits	457.87	1	<0.001	0.09	0.00		

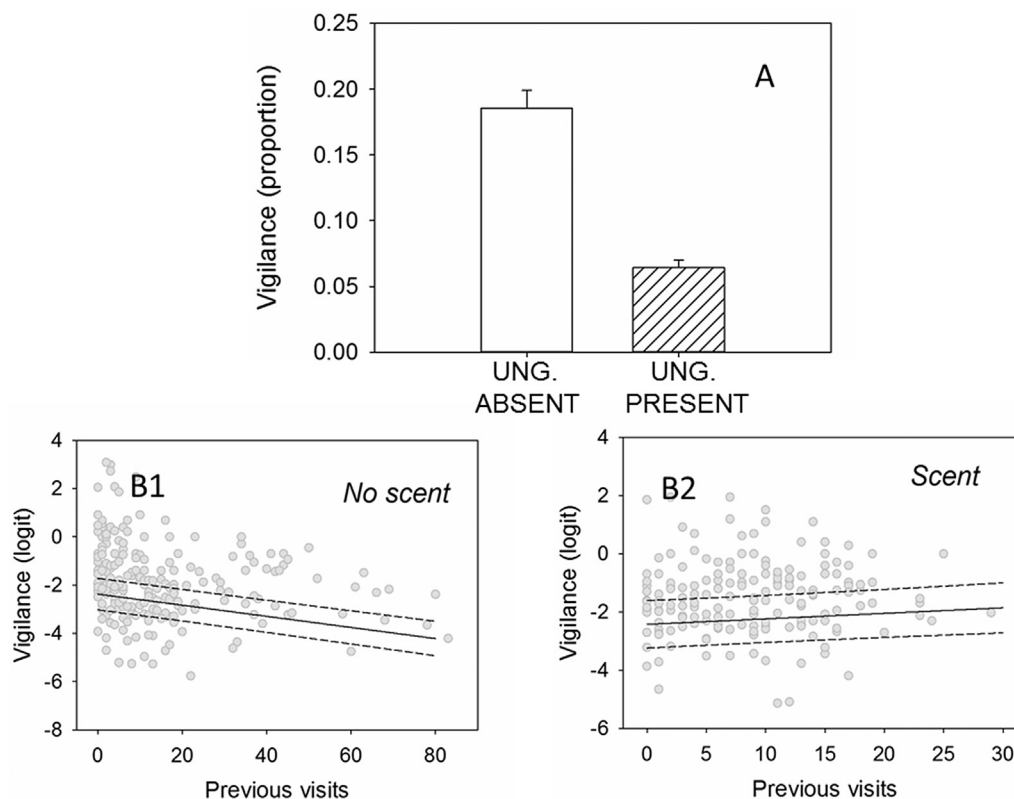


Fig. 1. (A) In the presence of ungulates mice spent less time in vigilant behaviors. (B) Predation risks showed interactive effects with previous experience. (B1) In control trees, rodents decreased the proportion of time spent vigilant throughout the night (B2) while they maintained a baseline vigilant behavior in trees treated with predator odor. Bars represent mean (+SE). Lines are regression models with 95% confidence intervals.

effect on time devoted to vigilance, but it interacted with the effects of previous experience. In control trees, not provided with scent, vigilance decreased with previous foraging experience, whereas no significant trend was found in trees provided with the scent treatment (Table 1, Fig. 1 B1, B2).

The number of foraging events made by intruders did not differ between experimental treatments (0.30 ± 0.1 number of visits per tree on average). In general, mice tended to display more vigilant behaviors when intruders were present (Table 2).

Manipulated acorns were dispersed more likely when the focal individual spent less time vigilant (estimate = -6.48 ± 0.00 , $P < 0.01$, $R^2_m = 0.18$, $R^2_c = 0.40$), and these effects were stronger in the absence of ungulates (Fig. 2). As a result, despite the fact that

mice spent less time vigilant in the presence of ungulates, mobilization rates were similar between enclosure treatments (0.18 ± 0.11 and 0.13 ± 0.11 , in the presence and absence of ungulates, respectively).

4. Discussion

Our results show that inter-specific competition for acorns and predation risks can have significant effects on mouse foraging behavior, and hence on acorn dispersal. These findings support the idea that the attributes of interaction networks in which plant-animal encounters occur affect seed dispersal outcomes (Bronstein, 1994; Herrera and Pellmyr, 2009; Bascombe and

Table 2

Results of Spearman's correlation tests between the number of previous visits by intruders and the components of the foraging behavior of Algerian mice (*Mus spretus*). Boldface indicates significant results.*Marginally significant.

Response	Treatment	rho	P
Event duration	Overall	0.23	0.04
	Ungulates (No)	0.12	0.03
	Ungulates (Yes)	−0.03	0.46
	Scents (No)	0.08	0.06
	Scents (Yes)	−0.04	0.93
Vigilance	Overall	0.16	<0.01
	Ungulates (No)	0.04	0.47
	Ungulates (Yes)	0.09	0.02
	Scents (No)	0.15	<0.01
	Scents (Yes)	0.18	<0.01
Acorn handling	Overall	−0.07	0.03
	Ungulates (No)	−0.05	0.39
	Ungulates (Yes)	−0.06	0.14
	Scents (No)	−0.08	0.06*
	Scents (Yes)	−0.05	0.30

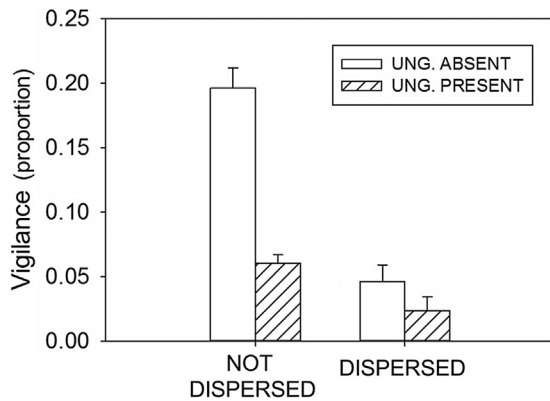


Fig. 2. When Algerian mice spent more time in vigilant behaviors, the probability of acorn mobilization was lower. These effects were stronger in the absence of ungulates. Bars represent mean (+SE).

Jordano, 2007). In addition, our work suggests that mice integrate direct cues of risk and competition with indirect ones related to habitat structure while foraging. Thus, in line with previous work (Cortés and Uriarte, 2013), our results underscore that incorporating landscape perception by animals will improve our understanding of the behavioral mechanisms underpinning the dispersal services they provide.

The fact that the frequency of visits by intruders was similar between treatments suggests that the presence of ungulates did not result into relaxed intra-specific competition in spite of an impoverished habitat quality for rodents (Muñoz et al., 2009). Ungulate presence was only linked to increased inter-specific competition for acorns. According to our hypothesis, lower *per capita* acorn availability would force mice to forage more efficiently promoting a scatter-hoarding behavior and, hence, improving the dispersal services provided to oaks (Theimer, 2005). However, this was only partially fulfilled. In the presence of ungulates, mice focused their foraging behavior on food acquisition at expenses of vigilant behaviors. Nonetheless, a more efficient foraging behavior did not imply enhanced mobilization rates. The proportion of offered acorns mobilized rather than consumed *in situ* was similar between enclosure treatments. Such mismatch may respond to unaffordable predation risks during acorn transportation. The presence of ungulates results in large proportions of open land cover (Muñoz et al., 2009), which implies low availability of safe

microhabitats for rodents (Díaz, 1992; Tew and Macdonald, 1993; Muñoz et al., 2009; Perea et al., 2011a). Hence, although transporting acorns outside tree canopies may be an efficient foraging strategy to safeguard them for winter consumption (Steele et al., 2014), lack of anti-predatory cover may have discouraged mice from doing so (see Morán-López et al., 2015b for similar results).

Overall, our results show that mice are able to adapt their foraging behavior to acorn availability. However, low *per capita* acorn availability does not warrant enhanced dispersal services. Scatter-hoarding is a step-wise process that involves subsequent foraging decisions (1) ignore or manipulate the encounter seed (2) consume it *in situ* or carry it away (3) how far to carry it, and (4) whether to eat the mobilized seed or store it (Wang et al., 2013). During this process, rodents balance the costs and benefits of each foraging decision (Lichti et al., 2017). Only if mobilizing and storing seeds results beneficial across all foraging decisions, rodents' activity will promote oak recruitment. Therefore, if habitat structure constrains mouse movements, and consequently cache protection strategies, a more efficient foraging behavior may not imply enhanced acorn dispersal.

Regarding intra-specific competition, mice adapted their foraging behavior to the presence of conspecifics (see Sunyer et al., 2013 for similar results). In contrast to what occurs in the presence of ungulates, when facing a situation of high intra-specific competition, rodents spent more time vigilant, probably patrolling and checking the acorns to prevent them being pilfered (Dally et al., 2006), as well as trying to chase away possible intruders (pers. obs.). In this case, mice displayed a more vigilant behavior in order to avoid acorn pilferage. It is likely that a higher investment in vigilance would also entail cache protection strategies such as enhanced dispersal distances and acorn deposition in areas of low rodent activity (Moore et al., 2007; Perea et al., 2011b). Unfortunately, our data does not allow us to test this hypothesis.

Manipulation of the risk of predation did not have significant pure effects on rodent foraging behavior, but modulated the effects of previous experience. In control trees, where risk perception was low, mice confidence increased throughout the night resulting in decreased vigilance. In contrast, when faced to genet odor, they maintained a baseline vigilant behavior. Responsiveness of mice to genet presence have been previously documented (Díaz et al., 2005; Navarro-Castilla et al., 2017a), as well as responses of other rodents to direct cues of predation risk (review in Caro, 2005). Nonetheless, this would be the first demonstration (at least in field conditions) of how perceived risk may suppress the benefits of self-confidence acquired by experience (Caro, 2005). Contrary to our expectations, increased risk did not imply enhanced mobilization rates, but the opposite. Similarly to what occurred with ungulate presence, mice may have not transported seeds to safe microhabitats because these were scarce or absent in tree surroundings. Our results are in line with previous work, which points to the lack of shrub cover as one of the main factor limiting oak recruitment in dehesas (Smit et al., 2008; Morán-López et al., 2016).

It is important to note that although fixed manipulative treatments showed significant effects on event duration and time devoted to acorn manipulation, the proportion of variance explained was marginal in comparison to random individual effects. These effects, most likely due to longer-term effects of individual's age, sex or territorial status (Crane and Ferrari, 2013; Godsall et al., 2014; Navarro-Castilla and Barja, 2014a), could not be analyzed because we used animal marks not permanent nor visible in recordings (small haircuts). Future work based on more suitable marks (e.g. transponders; Godsall et al., 2014) will help at disentangling the relative effects of these individual-level 'fixed' characteristic in mouse foraging responses.

5. Conclusions

Overall, our results show that successful acorn dispersal depends, at least partly, on relationships between plant and animals that are beyond the oak-rodent mutualism. Competition for seeds with ungulates as well as predation risk modified mice foraging behavior, and consequently, the probability of acorn mobilization. Therefore, any conservation policy aimed at restoring natural regeneration of oaks should take into account the interaction network in which oak-rodent mutualisms are embedded. Moreover, our work points out that mice incorporate direct and indirect cues of risk when taking their scatter-hoarding foraging decisions. This results in a highly flexible foraging behavior that depends on individual and previous experience effects. Incorporating such source variation into models will help at translating ecological noise into behavioral mechanisms driving acorn dispersal.

Authors' contribution

Diego Gallego-García visualized video-recordings and draft the first version of this article.

Teresa Morán López, collected field data, analyzed it and led the revised version of the manuscript.

Ignasi Torre, Álvaro Navarro Castilla and Isabel Barja collected field data and revised the manuscript.

Mario Diaz, conceived the experimental design, revised the article and served as the led for the project.

All authors approved the final version of the article.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2017.07.002>.

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