

**Context dependency in acorn predation and dispersal
by *Apodemus sylvaticus* in Mediterranean oak forests:
the role of seasonality, spatial heterogeneity and
animal-animal interactions**

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Tesis doctoral

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Variabilitat en la depredació i dispersió d'agllans per *Apodemus sylvaticus* en boscos Mediterranis d'alzina: el rol de l'estacionalitat, l'heterogeneïtat espacial i les interaccions animal-animal

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*“Look deep into nature,
and then you will understand everything better.”*

- Albert Einstein -

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RESUM

La biodiversitat que observem resulta d'una complexa història evolutiva d'interaccions entre els organismes. Les interaccions planta-animals en són un cas paradigmàtic, des de relacions antagòniques a mutualistes, però determinar-ne el resultat pot ser complicat, com en el cas de la dispersió de llavors per rosegadors. Moltes espècies de rosegadors són àvids consumidors de llavors, però també actius dispersors, inclús emmagatzemant-ne per al posterior consum, potencialment afavorint la dispersió i regeneració de l'espècie amb la que interactuen. Per això molts estudis s'han centrat en aquesta interacció, tot i que poques vegades s'ha considerat la influència que pot tenir la gran variabilitat temporal i espacial del context on es dona.

L'objectiu principal d'aquesta tesi és estudiar com els patrons de dispersió/depredació d'agllans per rosegadors poden estar influïts per la variabilitat del context en el que té lloc i determinar com pot afectar el reclutament de les espècies sobre les que actuen. Amb aquest fi hem utilitzat un model d'estudi paradigmàtic dels ambients Mediterranis: el ratolí de bosc, *Apodemus sylvaticus*, com a dispersor i depredador d'agllans en un bosc mixte de roure (*Quercus pubescens*) i alzina (*Quercus ilex*) al Parc Natural de Collserola. Hem mostrejat intensivament la població de rosegadors a la zona d'estudi i altres variables ambientals (producció i abundància d'agllans, coberta de vegetació, furgades de senglar), així com el reclutament de plàntules de *Quercus*. També hem analitzat els patrons de dispersió/depredació d'agllans per rosegadors mitjançant l'enregistrament del seu comportament i el seguiment d'agllans marcats.

Els nostres resultats indiquen que les dinàmiques demogràfiques d' *A. sylvaticus* estan condicionades per la disponibilitat d'agllans, amb importants davallades estivals en l'abundància degut a la sequera i l'escassetat d'aliment. A més, les diferències fenològiques en la producció d'agllans entre roure i alzina també afecten les decisions dels rosegadors, que canvien les seves preferències per l'espècie més abundant. Per altra banda, hem documentat l'efecte de nivells tròfics superiors (carnívors) en el destí de les llavors mitjançant canvis en el comportament dels rosegadors, així com efectes de competidors per aquest recurs (senglars i conspecifics) en els patrons de dispersió/depredació d'agllans. L'activitat dels rosegadors també juga un paper important en l'establiment de plàntules de *Quercus*, com a dispersors, movent principalment agllans de sota els arbusts cap a zones més obertes en aquests boscos d'elevada densitat, però també com a "lladres" d'agllans, reduint les oportunitats de reclutament per a la planta. De fet, la distribució espacial de plàntules en la zona d'estudi està determinada principalment per la

disponibilitat d'aglans, mentre que el possible efecte protector dels arbusts no té tanta importància com esperàvem prèviament, degut a les característiques del bosc (coberta arbòrea densa).

Aquesta tesi documenta que la interacció entre planta i rosegadors pot ser molt variable depenent del context on es dona, de manera que el paper dels rosegadors com a dispersors i depredadors d'aglans en boscos Mediterranis de *Quercus* pot diferir en funció de l'estructura del bosc (per exemple deveses vs. boscos tancats). Aquesta variabilitat temporal i espacial es deu principalment a la flexibilitat comportamental dels rosegadors, que adapten les seves decisions al context de cada lloc i moment. En canvi, hem documentat altres comportaments amb una tendència més fixa, com la preferència per llavors grans. En aquest sentit, aquests comportaments més fixes poden exercir pressions selectives importants sobre els trets vitals de la planta, mentre que comportaments més variables no tindran un efecte tant clar. Estudis futurs centrats en aquesta interacció entre planta i rosegadors haurien de tenir en compte aquesta variabilitat temporal i espacial, així com les interaccions assenyalades en el nostre estudi amb altres animals de la xarxa tròfica (carnívors i competidors).

SUMMARY

Earth's biodiversity results from a complex evolutionary history of interactions among organisms. Plant-animal interactions are a paradigmatic example of such ecological relationships, from antagonistic to mutualistic relationships, although determining its result might be difficult, like in the case of seed dispersal by rodents. Many rodent species are avid seed consumers, but also active dispersers, caching seeds in burrows for further consumption, potentially contributing to the dispersion and regeneration of the species with which they interact. Thus, many studies have focused on this interaction, although the influence of the great spatial and temporal variability of the context where it occurs has not been generally considered.

The main objective of this thesis is to assess how the acorn predation/dispersal patterns by rodents may be influenced by the contextual variability, and to determine how this variability might affect the recruitment of the species with whom they interact. To that end we have used a well-known study model paradigmatic of Mediterranean environments: the wood mouse, *Apodemus sylvaticus*, as seed predator and disperser of acorns in a mixed oak forest of Holm oak (*Quercus ilex*) and Downy oak (*Quercus pubescens*) in the Collserola Natural Park. We have intensively monitored the rodent population in the study area, some environmental factors (acorn production and abundance, vegetation cover, wild boar rooting), and oak's seedling emergence. We have also analyzed the acorn predation/dispersal patterns of rodents by recording their foraging behaviour and monitoring tagged acorns.

Our results show that the demographic dynamics of *A. Sylvaticus* are conditioned by the availability of acorns, with important population declines in the summers, due to the effects of drought and food scarcity. Moreover, the differences in seeding phenology between *Q. ilex* and *Q. pubescens* also affect rodent's foraging decisions, as they change their seed preferences for the most abundant species. We have also documented an effect of upper trophic levels (carnivores) on seed's fate by influencing rodent's behaviour, as well as effects from competitors for that resource (wild boars and conspecifics) on the acorn predation/dispersal patterns. Rodent's activity also plays an important role in oak's seedling establishment, as seed dispersers, removing many acorns from under shrubs towards open sites in these close canopy forests, but also as seed pilferers, reducing the recruitment opportunities of oaks. In fact, the spatial distribution of oak seedlings in the study area is mainly determined by the availability of acorns, while the potential nursing effect of shrubs does not have such an important effect as we had previously anticipated, due to the forest characteristics (dense tree canopy).

This thesis documents the great context dependent variability in the interaction among plants and rodents, so that rodent's role as acorn predators and dispersers in Mediterranean oak forests may be very different according to the forest structure (e.g. savannah-like forests vs. close canopy forests). This spatial and temporal variability occurs mainly due to the behavioural plasticity of rodents, which adapt their foraging choices to the context of every place and moment. On the other hand, we have also documented other behaviours that show a rather fixed trend, such as the preference for bigger and sound acorns. In this sense, these more fixed behaviours might represent important selective pressures on the life history traits of the plants they interact with, while more variable behaviours will not have such clear effect. Further studies focussed on this interaction among plants and rodents should consider this great temporal and spatial variability, as well as the interactions with other animals of the trophic web shown in our study (carnivores and competitors).

GENERAL INTRODUCTION

Seed dispersal by animals: a paradigmatic plant-animal interaction

Earth's biodiversity results from a complex evolutionary history of interactions among different species and groups of living organisms. Currently, there is a huge array of interactions among species, ranging from antagonistic to mutualistic (Labandeira 2002), which are the basis for ecosystem functioning. One of the most fundamental problems of these ecological interactions is predicting how their strength and outcome change in time and space (Agrawal et al. 2007). Plant-animal interactions are a paradigmatic example of such ecological relationships. Many animals depend on plants for cover, nesting and foraging (Price 2002), and many plants depend on animals for the dispersal of pollen and seeds (Herrera 2002). In many systems, plants and animals have coevolved in a scenario of complex mutualistic and antagonistic interactions, which is currently a topic of intensive research in the fields of ecology, evolution and animal behaviour. For instance, animals use fruits as food, while plants use frugivore animals as vectors for seed dispersal, a crucial life-history process of plants (Stiles 2000). This apparent mutualistic interaction, becomes less straightforward when animals use seeds as food and they also disperse and cache (scatter-hoard) them for further consumption (Vander Wall 1990). In that case, the outcome of the interaction is not easy to determine, given that it depends on many variables, as the costs/benefits of seed searching, seed selection and seed caching for the animal, or on the balance of seeds predated vs. successfully dispersed for the plant (Zwolak and Crone 2012). Thus, determining the final outcome of that kind of interactions is a subject of debate and intensive research in the field of plant-animal interactions (Howe and Miriti 2000, Wang and Smith 2002).

There is a huge variety of seeds in nature regarding their size, shape, and chemical composition (Leishman et al. 2000, Hulme and Benkman 2002). Resulting from a long life-history evolution, each plant species has developed certain seed attributes and strategies to maximize the chances of seeds to become new plants, a process highly conditioned by the likelihood of successful seed dispersal (Herrera 1987, Beck and Vander Wall 2010, Vander Wall 2010). In fact, seeds of different plant species have evolved converging into a similar set of traits as adaptations to the same dispersal vector (Forget and Milleron 1991): from small seeds with specific structures to enable wind dispersal (anemocory), to those that are passively or actively dispersed by animals (zoocory) (see Wilson and Traveset 2000). Besides this link between the seed dispersal syndromes and the seed traits evolved in different plant species,

there is also a significant intraspecific variability of seed traits. Seed dispersing animals may contribute to generate and maintain such intraspecific variability by preferentially dispersing certain seed phenotypes of a given plant species (Vander Wall 2010). For example, Muñoz et al. (2012) found a relationship between the preferences of a disperser for some particular seed shape and the variability of this seed trait in the population of the dispersed plant, so that morphologies with a lower dispersal probability were less frequently represented within the range of seed phenotypes in the plant population.

Active seed dispersal by animals (mainly vertebrates and ants; Stiles 2000) is a paradigmatic example of animal-plant interactions that involves the interplay among different ecological and evolutionary processes (e.g. plant history traits selection, animal behaviour, phenological matching). The consequences of such interaction are of paramount relevance for the dynamics of plant communities (Fenner 2000, Herrera and Pellmyr 2002).

Scatter-hoarding rodents: friends or enemies of plants?

Rodents and plants, a love/hate story

Rodents have colonized and adapted to a great variety of habitats, from dry deserts, to wet tropical forests, and are widespread in a vast range of latitudes and altitudes (e.g. Heske et al. 1994, Forget 1990, Unnsteinsdottir and Hersteinsson 2011). Rodents play a fundamental role in ecosystem functioning because, on the one hand, they structure the base of many trophic webs as common prey for a huge array of predators (reptiles, birds and mammals; Korpimäki et al. 1991, Kotler et al. 1993, Torre et al. 2002, Cheveau et al. 2004). Rodent's rapid reproductive cycle allows for population recovery and maintenance although the great predator pressure (Montgomery 1989, Torre et al. 2002). Thus, rodents condition the occurrence of species from upper trophic levels, to the point that some rodent predators may show temporary migrations when rodent abundance is low (Cheveau et al. 2004). In the context of plant-animal interactions, many rodent species feed on seeds, and they are known to influence the population dynamics of many plant species due to their dual role as seed predators and dispersers (Vander Wall 1990, Hollander and Vander Wall 2004). Those rodent species that are prominent seed predators can decrease dramatically the reproductive output of plants, thus reducing their recruitment opportunities (Hulme and Benkman 2002). Nevertheless, several species, so called scatter-hoarding rodents, move and hoard (i.e. disperse) seeds to face adverse seasons with lacking resources (Forget 1990, Vander Wall 1990, Hollander and Vander Wall 2004). This foraging behaviour may benefit plants if dispersed seeds are not finally eaten, eventually promoting the successful recruitment of the plant (Herrera 2002, Gómez et al. 2008, Muñoz and Bonal 2011).

In that case, the relationship between plants and scatter-hoarding rodents may be considered as mutualistic.

However, categorizing an interaction between two species as mutualistic implies to evidence a mutual benefit for both parts. In the case of the interactions between scatter-hoarding rodents and plants, it is clear that rodents obtain immediate benefits from the plant by consuming seeds. From the plant's view, the mutualism would imply that dispersed seeds have greater recruitment chances than not dispersed seeds, and that this advantage overrides the losses of seeds finally predated by the rodent (Zwolak and Crone 2012). It is agreed that dispersed seeds may increase the avoidance of natural enemies, sibling interactions and the probability of finding physically suitable establishment sites (see Wilson and Traveset 2000, Stiles 2000, Herrera 2002). However, estimating the net benefits of scatter-hoarding rodents for plants is thorny given the variety of factors and stages involved in the plant recruitment process (Pulido and Díaz, 2005). Moreover, the spatial and temporal scales determining relevant ecological and evolutionary processes of individuals (e.g. reproductive success, energy acquisition, growth) are dramatically wider for a plant (e.g. tree) than for a small rodent. In other words, it is relatively easy to monitor and assess directly the fitness performance (i.e. reproductive success) of a rodent along its life-span (usually months or few years), as compared to a tree that lives centuries (e.g. oaks). Therefore, while the seeds produced by a tree in a year may determine the foraging opportunities of a given rodent, the dispersal chances of a plant may be determined by hundreds of generations of rodents predated and dispersing its seeds. In this scenario, it is hard to determine accurately the influence of rodents on the recruitment probabilities of a plant; the strength and outcome of the interaction strongly depends on whether the behaviour of scatter-hoarding rodents changes in space and time. Hence, determining if rodents are “enemies or friends of plants” requires analyzing the spatial and temporal variability of rodent's foraging behaviour.

Are rodent's seed foraging preferences fixed?

Most research on the interactions between plants and scatter-hoarding rodents has tried to disentangle the factors affecting the foraging decisions of rodents when facing seeds (e.g. predate, disperse, cache), usually focusing on how different seed traits may influence their preferences. In this context, rodents seem to prefer big-sized and nutritive seeds, which are more likely to be successfully dispersed, as opposed to smaller and thin-hulled seeds that are more likely to be consumed *in situ* (Celis-Diez et al. 2004, Wang and Chen 2009, Perea et al. 2012a, Rusch et al. 2013, Xiao et al. 2013). Rodents' decisions are usually framed within optimal

foraging models where decisions should maximize food intake and reduce foraging costs (Lima and Dill 1990, Brown and Kotler 2004, Jorge et al. 2012). For example, the preference for consuming smaller-sized seeds and caching the bigger ones owes to an optimization of the foraging time: smaller seeds require lower handling time than bigger ones, providing an immediate energy gain and allowing rodents to invest in dispersing and burying bigger and more nutritious seeds for future situations of food scarcity (Jorge et al. 2012, Rusch et al. 2013). Similarly, rodents also seem to prefer round seeds over bullet-shaped ones (Muñoz et al. 2012), sound seeds over infested by insect larvae (Muñoz and Bonal 2008a, Perea et al. 2012a, b), or certain seed species over others (Pons and Pausas 2007), as the preferred seeds provide a greater energetic reward relative to their transportation costs.

Optimal foraging models assume that animal foraging decisions can be highly context-dependent, leading to consider that the mutualistic or antagonistic nature of the interaction between scatter-hoarding rodents and plants can vary in space and time. In fact, the population dynamics of rodents and their foraging decisions are known to vary according to seed availability (Shimada and Saitoh 2006, Pérez-Ramos et al. 2008, Saitoh et al. 2008, Vander Wall 2010, Di Pierro et al. 2011), a food resource that may strongly change in space and time. Some authors have recently proposed that rodent's preferences for certain seed traits may change according to the stage of the decision-making process (manipulate or not, consume or disperse, dispersal distance, cache or not; Wang and Chen 2012, Wang et al. 2013) or their previous foraging experience (Muñoz and Bonal 2008b). Hence, the foraging decisions of scatter-hoarding rodents are quite intricate, to the point that many studies analyzing their interaction with plants encountered considerable amounts of unexplained variation, or even apparent contradictory results (e.g. farther dispersal distances for larger seeds in Jansen et al. 2002 vs. farther distances for smaller seeds in Brewer 2001), a special thorny issue in community ecology. This unexplained variance is sometimes treated as random noise, but the pendant challenge is determining to what extent it can be explained by spatial and temporal variability in the foraging behaviour of animals, and to what extent this variation may determine the outcomes of animal-plant interactions.

Few studies have approached explicitly the issue of spatial and temporal variation in the seed predation and dispersal patterns by rodents, as most efforts have been devoted to find fixed ecological laws or patterns (Agrawal et al. 2007). Hence, we still need to take a close look at the behavioural flexibility of scatter-hoarding rodents, the assessment of the factors involved, and the consequences for plants. In addition, another research gap concerns the direct evidences linking the variability of rodent's foraging decisions (i.e. seed predation/dispersal patterns) and the final establishment of seedlings. Most studies on seed dispersal behaviour by rodents have

rarely measured its actual contribution to seedling recruitment (but see Muñoz and Bonal 2011, Steele et al. 2011, Pérez-Ramos et al. 2013), while those studies centred in plant recruitment have rarely provided evidences on the role of the foraging behaviour by seed predators/dispersers.

Why studying oaks and wood mice in Mediterranean forests?

Oaks are one of the main tree species of the forests in the Mediterranean Basin (Blanco et al. 1997, Terradas 1999). They play a key ecological role as they produce big sized seeds (acorns), which are highly nutritious (Vander Wall 2001; Den Ouden et al. 2005), and are a precious food source for many animals such as rodents (e.g. the wood mouse, *Apodemus sylvaticus*; Gómez et al. 2008, Muñoz and Bonal 2011), ungulates (e.g. the wild boar, *Sus scrofa*; Focardi et al. 2000), insects (e.g. *Curculio spp.*, Bonal et al. 2010) and birds (e.g. *Garrulus glandarius*; Den Ouden et al. 2005). Oaks rely on scatter-hoarding by rodents and birds for the dispersal of their acorns. Avian dispersers (mainly *G. glandarius*) often provide a long-distance dispersal (Gómez 2003) important for colonizing new areas, while scatter-hoarding rodents provide a comparatively shorter dispersal that contributes to the maintenance of recruitment at microhabitat scale within the same forest (Vander Wall 2001). Oaks show a great interannual variability in the acorn crops, alternating years of low acorn production, with mast years (i.e. years with synchronic massive production of acorns; Kelly and Sork 2002, Espelta et al. 2008, Fernández-Martínez et al. 2012). This leads to a high temporal variability in acorn availability on the ground (timing and quantity), what make oaks an ideal study model to assess the spatial and temporal variability in rodent's foraging choices (Figure 1). In addition, the coexistence of different oak species in Mediterranean forests enables to test the effects of different seed characteristics (e.g. size, species and nutritional content), and different seed drop phenology on the foraging patterns of rodents and recruitment success of oaks (Figure 1). On the other hand, the wood mouse, *Apodemus sylvaticus*, is the main acorn predator and disperser in European oak forests (Den Ouden et al. 2005, Gómez et al. 2008, Perea et al. 2011a). They are widely distributed in all Europe and are very common in Mediterranean environments (Montgomery et al. 1999). Wood mice populations and activity are constrained by specialist predators like the common genet (*Genetta genetta*, Torre et al. 2002), and by large ungulates like the wild boar (*Sus scrofa*), that may compete with mice for acorns and may reduce habitat quality due to rooting activity (Focardi et al. 2000, Pulido and Díaz 2005, Muñoz et al. 2009). Both genets and wild boars are abundant in Mediterranean oak forests (Focardi et al. 2000,

Virgós et al. 2001) and have the potential to interact directly with wood mouse foraging behaviour, and thus indirectly with their influence on oaks' recruitment (Figure 1).

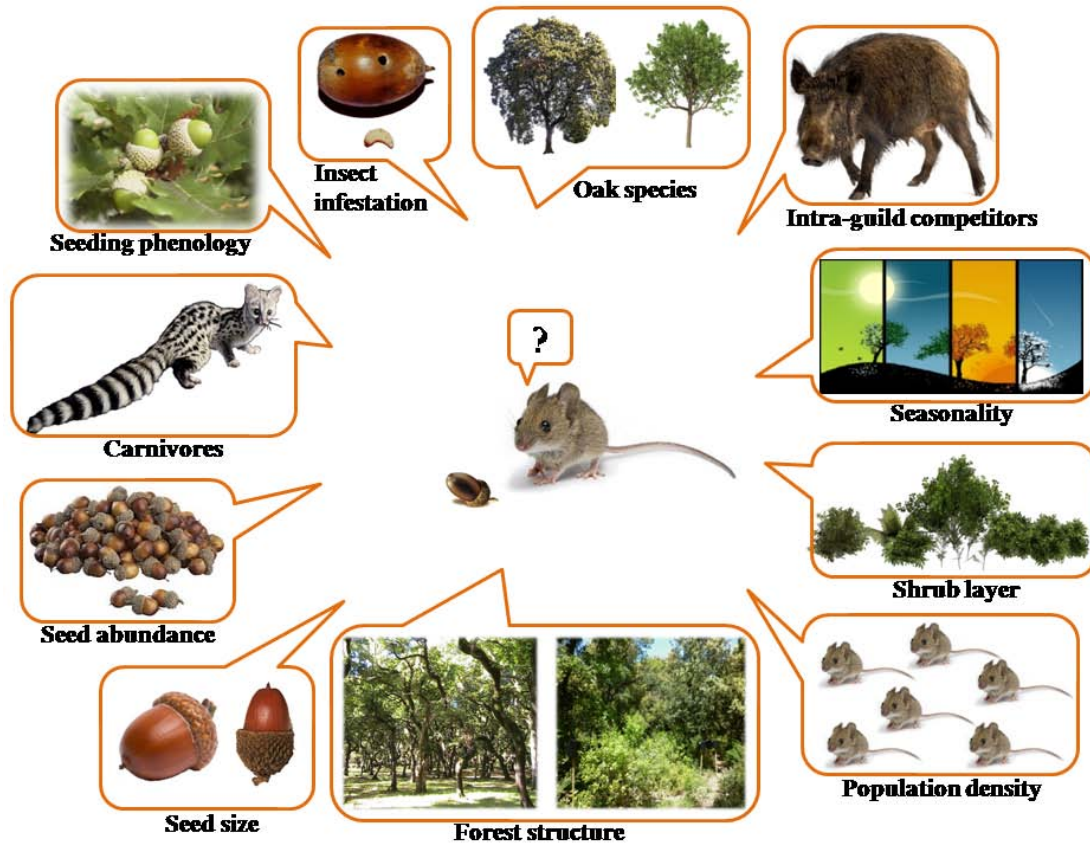


Figure 1. Potential factors influencing the acorn predation and dispersal behaviour of wood mice in Mediterranean oak forests. Seed traits (seed size, insect infestation and oak species), environmental factors (seasonality, seeding phenology, seed abundance, shrub density and forest physical structure), and interactions with other animals (carnivores, interspecific and intraspecific acorn competitors) may determine the foraging decisions of wood mice and their acorn dispersal and predation patterns.

In addition to the intrinsic variability in acorn production, it must be stressed that Mediterranean climate is highly heterogeneous and unpredictable (Blondel and Aronson 1999; Scarascia-Mugnozza et al. 2000), marked by severe summer droughts (Rosário and Mathias 2004, Espelta et al. 2008), with important fluctuations in the availability of resources (Torre et al. 2002, Rosário and Mathias 2004, Espelta et al. 2009a). Rodents in Mediterranean habitats have to adapt their biology, behaviour and foraging strategies, to this changing environment. For example, Mediterranean wood mice populations show their lowest densities in summer (due to the effects of drought) and the maximum in winter-spring (Fons and Saint-Girons 1993, Torre et al. 2002, Rosário and Mathias 2004), whereas northern European populations show the lower

densities during winters (Montgomery 1989, Fernandez et al. 1996; Unnsteinsdottir and Hersteinsson 2011). The environmental heterogeneity of Mediterranean habitats provides a perfect scenario to assess the influence of the context on rodent's seed choices, even more considering the broad variety of oak forest types that we may find according to their vegetation structure (Figure 1). For example, the environmental pressures imposed to rodent populations and behaviour are probably very different in a savannah-like oak forest (with a low density of oaks and a scarce understory; e.g. Pulido and Díaz 2005, Muñoz et al. 2009, Smit et al. 2009, Muñoz and Bonal 2011), than in a dense forest with a continuous tree canopy and a rich and abundant shrub layer (i.e. the study area). Previous studies have analysed the acorn dispersal behaviour by rodents in Mediterranean environments, focusing on the influence of plant cover (Pérez-Ramos et al. 2008, Perea et al. 2011b), ungulate presence (Focardi et al. 2000, Muñoz et al. 2009), seed species (Pons and Pausas 2007), seed size (Muñoz and Bonal 2008a), seed shape (Muñoz et al. 2012) or seed's insect infestation (Perea et al. 2012b). However, the research in seed dispersal ecology still needs to explicitly explore how the variability in such environmental factors and seed attributes may affect rodent's foraging decisions, seed dispersal patterns, and ultimately oak's recruitment.

Variability in wood mouse foraging behaviour

Based on the knowledge of the ecology of rodent-oak interactions in the Mediterranean systems, we have established three potential sources of variability in the foraging preferences by scatter-hoarding rodents that deserve research attention: i) **temporal variability**, ii) **spatial variability**, and iii) **interactions with other animals**

Temporal variability

Acorn crops usually experience great interannual variations that have been extensively documented in the literature (e.g. masting; reviewed by Kelly and Sork 2002). Some studies have assessed the effects of the high acorn availability of mast years on the decisions of scatter-hoarding rodents (Shimada and Saitoh 2006, Saitoh et al. 2008, Vander Wall 2010). However, acorn availability may also change within the same year due to the phenology of acorn drop. Most importantly, the phenological differences among coexisting oak species within the same seeding season also determine seasonal variations in the quantity and quality of acorns available within the same year (Espelta et al. 2009a, b). Hence, rodents must frame their foraging decisions in a changing scenario of acorn availability within the same seeding season, and thus

they are expected to adapt and respond to these short-term changes. Moreover, the small rodent populations also experience rapid and dramatic changes in abundance (Montgomery 1989, Fernandez et al. 1996, Torre et al. 2002). This results in a great temporal variation of intraspecific competition and density-dependent effects that may be additional sources of variation in their foraging behaviour within the same seeding season.

Spatial variability

Microhabitat structure is a key factor for small rodents, and may be very heterogeneous at different spatial scales. Since plants offer an important protective cover that reduces predation risk and provides suitable thermal and hydric conditions (Schradin 2005, Muñoz et al. 2009, Perea et al. 2011b), small rodents often concentrate their activity under plants. This may impose spatial shifts to several aspects of rodents' behaviour, such as the time invested in seed selection, the decision of predating or dispersing seeds, or the microhabitat of dispersed seeds (Pons and Pausas 2007, Pérez-Ramos et al. 2008, Muñoz et al. 2009, Beck and Vander Wall 2010). Additionally, scatter-hoarding rodents are well-known pilferers of seed caches from other conspecifics (for a revision, see Vander Wall and Jenkins 2003), being pilferage a key aspect that strongly influences their seed predation and dispersal decisions (Muñoz and Bonal 2011). Since rodent and acorn abundance are expected to change at small scales, the conspecific competition for seeds, and particularly the pilferage rates, may also strongly change in time and space. Similarly, other factors that might affect rodent foraging decisions, such as predator presence, or seed abundance, can also strongly vary in space. As a result, the seed predation and dispersal patterns by rodents could change at a small spatial scale. On the other hand, the recruitment patterns of oaks may also change at microhabitat scale due to seed and seedling requirements for germination and establishment, like soil moisture, light (Beckage and Clark 2003), sometimes related with nurse shrubs (Gómez-Aparicio et al. 2005). Besides some of these processes have been well documented in different experiments (e.g. microhabitat requirements for seeds and seedlings, effects of nurse shrubs, seed predation and dispersal patterns by rodents), there is a lack of direct evidences linking the spatial patterns of natural recruitment to the spatial patterns of rodents' behaviour.

Interactions with other animals

Rodents might be strongly conditioned by the presence of potential predators and competitors for food. On the one hand, besides the obvious direct effects of predation on the

demography of rodents, predator presence might also affect the behaviour and foraging decisions of scatter-hoarding rodents. In fact, optimal foraging models consider explicitly the predation risk as a critical factor determining the foraging strategies of animals (Lima and Dill 1990, Brown and Kotler 2004). This means that a predator of scatter-hoarding rodents could indirectly influence the fate of dispersed seeds. On the other hand, wild boars' presence and rooting activity may have strong effects on rodents' populations and foraging behaviour. Thus, besides their direct impacts on oak recruitment by killing seedlings and predating acorns (Gómez and Hódar 2008), they may indirectly affect seed fate through changes in rodent's behaviour.

Research objectives of the thesis

The main objective of the thesis is to assess the context-dependency of acorn predation and dispersal patterns by scatter-hoarding rodents in relation to changing environmental factors in time and space like seed abundance, conspecific abundance, microhabitat structure, presence of predators and seed competitors. Ultimately, we wanted to assess how this variability influences the spatial patterns of oak recruitment. As study model we have used the wood mouse, *Apodemus sylvaticus*, in Mediterranean mixed-oak forests. To approach this general objective, we have organized the thesis in four thematic chapters:

In the **first chapter**, we assessed the changes in space and time of wood mice populations in Mediterranean oak forests. The population size (i.e. number of rodents) in a given moment or site reflects the potential number of predators and dispersers of acorns, but also the potential number of conspecific competitors for acorns. We specifically tested the relative contribution of seasonality in acorn abundance, vegetation structure, and the presence of wild boars on the demographic parameters of wood mouse populations like abundance, survival, body mass and spatial distribution.

In the **second chapter** we investigated the temporal changes in the patterns of seed predation and dispersal by wood mice in response to temporal variations in seed availability and quality in a mixed-oak forest with two co-occurring oak species (*Quercus ilex* and *Q. pubescens*) that show different seeding phenologies. We wanted to determine whether wood mouse foraging decisions were fixed along the seeding season or, by contrast, they adapt their behaviour to the phenology of oaks.

In the **third chapter**, we experimentally studied the influence of perceived predation risk and conspecific competition on the seed predation and dispersal decisions by wood mice.

We aimed to test whether a species from upper trophic levels (i.e. a specialised carnivore, *Genetta genetta*) could indirectly affect acorns' fate by influencing the rodent-oak interaction.

Finally, in the **fourth chapter**, we assessed the spatial relationships among seed foraging patterns by wood mouse, acorn abundance, wild boars rooting activity, and shrubs' presence, and their link with the spatial patterns of oak seedlings recruitment.

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STUDY SITE AND SPECIES

This field research was conducted from 2010 to 2012 at Collserola Natural Park (Barcelona, Spain; 41°24'N, 2°6'E), a typical Mediterranean-type coastal massif. The climatology of the study area for that period was characterized by a mean (here and after mean \pm SE) annual temperature of 15.8 ± 0.4 °C, ranging from 2.8 in winter to 31.6 °C in summer, and a mean annual precipitation of 688 ± 112 mm, marked by strong summer droughts (climatic records obtained from Fabra meteorological observatory, in Collserola Natural Park). The study site was the forest of Can Balasc, a Mediterranean mixed-oak forest dominated by the evergreen Holm oak, *Quercus ilex*, and the winter-deciduous Downy oak, *Q. pubescens* (Espelta et al. 2008, Espelta et al. 2009). The forest understory presents a generally abundant shrub layer, mainly composed by *Pistacia lentiscus*, *Arbutus unedo*, *Viburnum tinus*, *Quercus coccifera*, *Rhamnus alaternus*, *Phillyrea latifolia* and *Erica arborea*, with a ground-layer vegetation dominated by *Hedera helix*. The seeding season of the two temperate oaks in the study area spans autumn-winter, but *Q. ilex* acorns are produced *ca.* one month later than *Q. pubescens* (Espelta et al. 2009, Fernández-Martínez et al. 2012). Besides this differences in phenology, *Q. ilex* acorns are smaller than those of *Q. pubescens* (respectively, mean weight of 0.5 ± 0.1 g vs. 1.1 ± 0.2 g in Espelta et al. 2009), but have a higher fat content (respectively, 4.0 ± 0.3 % vs. 1.5 ± 0.2 %; $t_{31} = 7.8$, $p < 0.001$, own data). Acorns mature within one year and are dropped on the ground once ripen (Espelta et al. 2008). Acorn germination takes place during the winter and seedlings usually emerge in March-April (González-Rodríguez et al. 2011).

During the seeding season, acorns are the main food source for scatter-hoarding rodents like the wood mouse, *Apodemus sylvaticus*, which predate and disperse them actively (Jensen and Nielsen 1986, Gómez et al. 2008, Muñoz and Bonal 2011). The wood mouse is the most abundant rodent in Mediterranean forests of the Iberian Peninsula (Torre et al. 2002) and one of the main acorn dispersers in European oak forests (Den Ouden et al. 2005, Perea et al. 2011). This rodent species is the preferred prey of specialised terrestrial carnivores like the common genet (*Genetta genetta*; Lodé et al. 1991, Hamdine et al. 1993, Virgós et al. 2001, Torre et al. 2003), a nocturnal small forest carnivore that is very common at the study area (Llimona et al. 2007). Wild boars, *Sus scrofa*, are also very abundant in the Collserola Natural Park (Cahill et al. 2003), and are also prominent acorn predators that may compete with wood mice (Focardi et al. 2000). Finally, acorns are also a food source for larvae of specialised insects such as curculionids (*Curculio sp.*). Adult females lay the eggs inside maturing acorns while they are still in the tree, and these infested acorns drop prematurely (Bonal and Muñoz 2007).

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PHOTOGRAPHIC APPENDIX



Image 1. Vegetation structure of the study area and the seed traps installed under oaks.



Image 2. Sampling point marked by a yellow wooden stake, with a Sherman trap (bottom-right), and several seed traps under oak coppices.



Image 3. Preparing the Sherman traps for a trapping session. Each trap was baited with a mix of flour and tuna in oil, and a piece of apple to avoid dehydration. A handful of hydrophobic cotton was also introduced so that captured mice could make a nest and keep warm until they were marked and released.



Image 4. Captured mice were taken from the Sherman traps using a plastic bag.



Images 5 and 6. Each captured mouse was weighed, and we also determined their sex using the anus-genital distance.



Images 7 and 8. Passive Integrated Transponder (PIT) tags were used to permanently mark the captured mice, applying them under the skin below the neck using a specialized syringe.



Image 9. We designed a simple but useful device that helped us immobilize the animal in order to mark it with more accuracy and reducing the manipulation time.



Image 10. Releasing a captured wood mouse after its manipulation.



Image 11. Releasing a captured wood mouse directly from the trap, after its manipulation.



Image 12. In order to assess the dispersal patterns of acorns by mice, we tagged several acorns with a 40 cm long wire with a bright flag attached at its end that enabled us to find them after being dispersed.



Image 13. Tagged acorns were placed inside a wire cage to ensure that only mice could remove them.



Image 14. To record the foraging behaviour of mice under three different smell treatments (Chapter 3), we installed night-vision cameras in different sampling points aimed towards the cage with the tagged acorns, and protected by a plastic box. Additionally, we attached two handfuls of cotton to the cage to apply the smell treatments.



Image 15. Image captured by the night-vision cameras of a wood mouse handling one of the tagged acorns.



Image 16. Image captured by the night-vision cameras of a genet smelling the cottons where the smell treatment (genet smell) had been applied.

CHAPTER 1

Seasonality in seed availability rules the population dynamics of a seed disperser: the case of wood mice, *Apodemus sylvaticus*, in Mediterranean oak forests

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SUMMARY

Small rodents play a key role in forest ecosystems as common prey, but also as prevalent seed consumers and dispersers. Hence, there is a great interest in disentangling the factors involved in their population dynamics. We conducted an intensive 2-year field study to test the relative role of seasonality in seed abundance, shrub cover and wild boar interference on the population dynamics of wood mice, *Apodemus sylvaticus*, in a Mediterranean oak forest. Wood mice demographic parameters were strongly influenced by the seasonal variations in acorn availability on the ground. Mice survival, abundance and body mass dropped drastically during summer owing to acorn scarcity, rising again in autumn, when acorn-fall begins. Specifically, we found a direct correlation between female abundance and the temporal changes in acorn availability on the ground. In contrast to studies conducted in sparse oak forests in drier environments, spatial variability in shrub cover and wild boars' foraging activity did not affect directly the population dynamics of wood mice, probably due to the presence of an abundant shrub layer and a closed canopy in our forest that enhance environmental conditions and provide shelter against predators and ungulates. This highlights that the relative importance of environmental factors and intraguild competition on rodent dynamics may be highly context-dependent, varying greatly among different forest types. Many studies have analyzed how oak recruitment depends on scatter-hoarding rodents, but little is known on how scatter-hoarding rodents depend on oaks (i.e. acorn crops). Our study suggests that the relationships between acorn dispersers and oaks can be more reciprocal than previously considered.

Key words: Acorns, *Apodemus sylvaticus*, Mediterranean, *Quercus ilex*, *Quercus pubescens*, rodents, *Sus scrofa*

INTRODUCTION

Small rodents play a crucial role in forest ecosystems. On the one hand, rodents are consumed by many predator species (reptiles, mammals and birds, Kotler et al. 1993, Torre et al. 2002, Cheveau et al. 2004), but their high reproductive rates allow a rapid population recovery and persistence (Torre et al. 2002). On the other hand, many rodent species are important seed predators and effective dispersers (Den Ouden et al. 2005, Muñoz and Bonal 2007, Perea et al. 2011a), eventually moving seeds to caches in optimal places for seedling emergence, thus promoting plant recruitment (Vander Wall 1990, Vander Wall 2001, Hollander and Vander Wall 2004). Consequently, the assessment of the main factors involved in the population dynamics of rodents has been a subject of major interest for research (Montgomery 1989a, Fernandez et al. 1996, Rosário and Mathias 2004).

Rodent populations often experience marked seasonal and interannual fluctuations, decreasing during the season with the more adverse climatic conditions and increasing in the favorable periods (Montgomery 1989a, Fernandez et al. 1996, Torre et al. 2002). However, the effect of climate usually interacts with other environmental variables such as resource abundance and intrinsic factors like density-dependent regulation. Thus, several studies have documented a positive association between increasing food availability and overwinter survival or population density (Montgomery 1989a, Montgomery et al. 1991, Díaz et al. 2010). In fact, in years of exceptionally high resource availability, breeding and population growth may continue even during the climatic adverse season (winter in many latitudes; Montgomery 1989a, Montgomery et al. 1991). In addition to these environmental factors, some studies have pointed out the importance of intrinsic factors like density-dependence on population dynamics due to negative effects of social interactions (e.g. breeding inhibition in females or exclusion of young males by aggressive adult males, Montgomery 1989b, Fernandez et al. 1996, Díaz et al. 2010). According to Unnsteinsdottir and Hersteinsson (2011) the relative importance of environmental vs. intrinsic factors on rodent abundance may vary depending on climate or habitat quality.

The wood mouse (*Apodemus sylvaticus*) is a common scatter-hoarding rodent in Mediterranean habitats of southern Europe (Montgomery 1999), and the most abundant in the Mediterranean forests of the Iberian Peninsula (Torre et al. 2002). It is an important predator and disperser of acorns (Den Ouden et al. 2005, Perea et al. 2011a) thus playing a key role in the regeneration patterns of oaks (Pulido and Díaz 2005, Gómez et al. 2008, Sunyer et al. in press). Wood mice show a great foraging plasticity, modifying their diet depending on the most abundant food source such as fleshy fruits, fresh plants' parts and even invertebrates (Khames and Aulagnier 2007, Unnsteinsdottir and Hersteinsson 2011, Sunyer et al. 2014). Nevertheless,

they are mainly granivores, and seed availability has been suggested as a limiting factor for wood mice populations (Montgomery et al. 1991, Saitoh et al. 2008, Díaz et al. 2010). Food availability can determine their home ranges, which are inversely proportional to habitat quality (Torre et al. 2002). Furthermore, males usually have wider home ranges to increase breeding opportunities, while females are more resource-dependent for reproduction efforts and often establish smaller good-quality territories, which are easier to defend from other females (Fernandez et al. 1996, Torre et al. 2002, Godsall et al. 2014).

The Mediterranean populations of wood mice are subjected to the heterogeneity and unpredictability of the Mediterranean climate (Blondel and Aronson 1999), marked by severe summer droughts and high temperatures (Espelta et al. 2008). Unlike central and northern Europe, in the Mediterranean Region summer is the most adverse season, because drought reduces resource availability (Herrera 1995, Torre et al. 2002, Rosário and Mathias 2004). Consequently, population size of wood mice decreases in summer (the non-breeding season) and reaches its maximum in winter-spring (Fons and Saint-Girons 1993, Torre et al. 2002, Rosário and Mathias 2004). Besides climate and food availability, interactions with other animals may also constrain the population dynamics of wood mice. On one hand, they must face a constant predation risk, especially from *Strix aluco* and *Genetta genetta* (reviewed by Torre et al. 2002). On other hand, big ungulates such as the wild boar, *Sus scrofa*, may have a negative effect on rodent populations as they compete for food resources (e.g. acorns), reduce habitat quality due to rooting activities, and may even predate small rodents (Focardi et al. 2000, Gómez and Hódar 2008, Muñoz et al. 2009). In this context, dense shrubs seem to function as protective cover against both rodent predators (Perea et al. 2011b, Rosalino et al. 2011) and wild boars (Muñoz et al. 2009). Nevertheless, the relative importance among acorn availability, wild boar presence and shrub cover on wood mouse population dynamics remains still seldom explored.

The main aim of this study has been to disentangle the relative importance of seasonality, acorn abundance, vegetation structure, and intra-guild competitors (i.e. wild boar activity) on the demography of wood mice in a Mediterranean oak forest. To that end, we intensively monitored a wood mouse population using capture-mark-recapture (CMR) techniques during 24 consecutive monthly trapping sessions, in two neighboring sites in a Mediterranean oak forest, one of them fenced to exclude wild boars. Additionally, we assessed the vegetation structure at a fine spatial scale, the acorn crops and the availability of acorns on the ground. We hypothesize that: i) the demographic parameters of *A. sylvaticus* (abundance, survival probability, and body mass) will be highly time-dependent, varying seasonally with acorn availability, ii) wood mouse abundance will be spatially aggregated according to shrub

cover and the abundance of acorns, iii) the demographic dynamics and the response to the abovementioned factors will differ between males and females, due to sexual differences in the breeding behavior, and iv) wild boars will negatively influence demographic parameters of wood mice, due to boar disturbance of rodent activity and to reduced habitat quality (acorn abundance).

MATERIALS AND METHODS

Experimental design

From June 2010 to July 2012, we intensively monitored the population of wood mouse at Can Balasc by capture-mark-recapture in monthly trapping sessions (total trapping effort: 12.672 trap-nights). We delimited a study area by marking permanently 132 fixed points with wooden stakes, each with an alphanumeric code, forming a grid so each stake was at a distance of 10 meters from each other. In order to assess the influence of wild boars on the population dynamics of rodents, ca. half of these points (65) were placed inside an ungulate enclosure protected by a 2 meter-high metallic fence, while the rest (67) were left outside the fence. We conducted monthly trapping campaigns of four nights with Sherman live-traps (23.5 x 8 x 9 cm; HB Sherman Traps Inc. Tallahassee, Florida USA). During each trapping campaign, we placed 132 traps (one at each marked point) baited with a mixture of flour and tuna in oil, and a piece of apple for hydration. All traps also contained a handful of hydrophobic cotton so that the captured rodents could make a nest to keep comfortable until they were marked and released (Muñoz et al. 2009, Sunyer et al. 2014). Each trapping campaign the traps were set for four consecutive nights at sunset (i.e. 20:00 hours GMT) and were checked every morning at sunrise (i.e. 07:00 hours GMT). Captured rodents were weighted, sexed and permanently marked with passive integrated transponder tags (MUSICC, AVID Identification Systems Inc.; size = 8 mm; weight = 0.06 g). Unique tags were implanted under the skin below the neck using a specialized syringe (AVID SUDS monoject) to individually identify each recaptured rodent. Once marked, individuals were released at their point of capture. The monitoring of the rodent population was conducted with a permit of the Collserola Natural Park authorities (num. 808), and following the guidelines of the American Society of Mammalogists (Sikes et al. 2011).

We quantified habitat quality at each capture point (i.e. 132 marked stakes). Specifically, we measured the shrub cover, known to influence rodent distribution and behavior (Montgomery et al. 1991, Muñoz et al. 2009, Rosalino et al. 2011), and also estimated acorn availability, which is the main food resource of *A. sylvaticus* during the seeding season. Shrub cover was measured as the percentage covered by shrubs in a circular area of 1 meter radius

from the stake. The availability of acorns on the ground was measured on a monthly sampling basis during almost a year round -September 2010 to June 2011- by counting all the ripe acorns on the ground within a circular area of 1 meter radius from each stake, and we recorded acorn species and condition (sound or infested by insects). Moreover, to assess the phenology of acorn drop we monitored the acorn production from trees in the stand. We installed four seed traps (i.e. 38-cm diameter buckets) under 40 similar sized adult oaks along the study area (20 oaks outside the wild boar enclosure and 20 inside) (see Sunyer et al. 2014). Seed traps were installed before the seeding season of the first study year (August 2010), and collected acorns during two complete seeding seasons (i.e. until all acorns had dropped). We visited seed traps every 15 days during the 2010 and 2011 seeding seasons. During each seed trap visit, we counted the number of sound and infested acorns dropped per tree.

Data analysis

We used capture-mark-recapture (CMR) models to estimate *A. sylvaticus* apparent survival and abundance according to their sex (male or female), the site (inside and outside the wild boar enclosure) and the season (autumn, winter, spring or summer, of each year). Our wood mouse trapping design followed Pollock's robust design (Pollock 1982), with four consecutive nights of trapping each month. The robust design considers secondary capture periods (i.e. our four consecutive nights) during which the population is closed to changes in abundance, and primary capture periods (i.e. monthly intervals) during which the population is open to changes due to mortality, recruitment, immigration, or emigration (Pollock 1982). Our study consisted of 24 primary periods (monthly intervals), each with 4 secondary periods (daily captures), for a total of 96 sampling occasions.

In this study we used the conditional likelihood formulation of the closed model (Huggins 1989) to obtain the estimates of our robust design model. We estimated the probabilities of capture at secondary period i in primary period j (p_{ij}) and recapture (c_{ij}). For the intervals between primary sampling periods i , we estimated the probability of apparent survival (S_i), the probability of temporary emigration from the study area (γ''_i) for an animal present in period $i - 1$ and surviving to period i , and the probability of an animal out of the study area in period $i - 1$ to survive and remain outside the study area to period i (γ'_i). Abundance (N_i) was obtained as a derived parameter.

We built a set of candidate models following an information-theoretic approach based on the AICc (Burnham and Anderson 2002, Mazerolle 2006). We formulated different models

based on biological hypotheses to determine the effects of season in each year (Season: 9 year x season combinations), exclusion of wild boar (Site: 2 types), and sex (Sex: males and females) on the model parameters (Table 1). The resulting set of candidate models (49 models) were fit with program MARK (White and Burnham 1999) within R using the RMark package (Laake et al. 2012, R Core Team 2013). We assessed the goodness of fit for the time-dependent Cormack-Jolly-Seber (CJS) model using program RELEASE ($\chi^2_{118} = 76.97$; $p = 0.99$; Burnham et al. 1987) and program U-Care ($\chi^2_{72} = 75.24$; $p = 0.37$; Choquet et al. 2009). The estimated \hat{c} value was respectively 0.98 and 1.03, thus we used a \hat{c} value of 1. We computed model-averaged estimates and variance-covariance matrices for all the parameters including abundance. Our CMR analysis was based on 580 *A. sylvaticus* individuals (259 males and 321 females).

Additionally, we used linear regression models to test the correlations between overall mice abundance of each sex in every trapping period and acorn abundance on the ground. In order to assess the differences in abundance between males and females, and between inside and outside the enclosure for the total number of mice, we also ran two respective paired t-student tests.

To assess the effects of the ungulate enclosure and the sampling season (autumn, winter, spring) on the number of sound acorns available on the ground we performed a GLMM with a Poisson distribution, including the trap location (stakes) as a random factor to control for potential spatial autocorrelation. To perform the analyses we did not include the summer because there are no ripe acorns on the ground during that season, and we only considered sound acorns, since infested ones are avoided by rodents (Muñoz and Bonal 2008). The GLMM were built using R packages lme4 (Bates et al. 2011) and model selection and multimodel inference was implemented using AICcmodavg (Mazerolle 2015).

To analyze the role of shrub cover on the capture success, we used GLMM with a binomial distribution and the capture points as a random factor. We tested the fixed effects of the season, the shrub cover (as a proportion, from 0 to 1), and the exclusion of wild boar, on the capture success of each trap (0 if it had not captured any mouse, or 1 if at least one mouse was captured), at every primary capture session (24 consecutive trapping sessions). We built a candidate set of GLMM, each testing for a specific biological hypothesis. We then compared the set of models according to the AICc, and extracted the estimate and confidence intervals of the different levels of each parameter using multimodel inference. Additionally, we also used a set of GLMM with a Normal distribution to test the effects of season, the exclusion of wild boar and the abundance of acorns on the weight of mice (log-transformed to adjust to a normal

distribution), excluding the juveniles (i.e. < 15 g). Again, the capture point was introduced as a random factor to control the spatial autocorrelation, but since they did not differ from the non-mixed models, we used the simpler ones (the models without the random factor).

Parameter	Factor	Hypothesis
S	Season	The survival of wood mouse individuals varies among seasons and years due to the different availability of resources and climatic conditions.
	Season + Site	Survival is influenced by the seasonal variability in resources availability and climate, but also depends on the habitat quality, conditioned by the activity of wild boar (competition for resources, rooting and eventual predation).
	Season + Sex	Survival is influenced by the seasonal variability in resources availability and climate, and differs between sexes due to differential energetic requirements.
p	Season + Sex	Wood mouse activity (and thus their capture probability) may vary depending on the seasonal differences in availability of resources and population density, and according to sex, due to their different behaviors regarding breeding, territory defense, and mate searching.
	Site + Sex	Wood mouse activity (and thus their capture probability) is determined by the habitat differences under the effects of wild boars, and differs between sexes.
c	Season + Sex	Recapture probability depends on seasonal and sexual differences in their activity as mentioned above.
	Site + Sex	Recapture probability depends on the habitat quality under the effect of wild boars, and sexual differences in their activity, as mentioned above.
γ''	Season + Sex	Emigration probability may differ among seasons, due to differences in the availability of resources and population densities, and between sexes due to their differential activity patterns.
	Site + Sex	Besides the effect of the sexual differences in behavior, emigration probability may be influenced by the habitat quality, determined by wild boar presence and activity (decline in availability of resources, direct effects on rodent's behavior and activity).
γ'	Season + Sex	Same as above
	Site + Sex	Same as above

Table1. Hypotheses considered for each parameter to construct the set of candidate Huggins robust design models for the analysis of CMR data with program MARK. The different hypotheses were constructed according to the published literature and study hypotheses.

To consider the potential influence of summer drought on the population dynamics of wood mice, we calculated a summer drought index: (mean temperature from June to August) –

0.33 x (mean rainfall from June to August) (see Espelta et al. 2008), for each of the three summers from 2010 to 2012. Monthly temperature and precipitation records from June 2010 to August 2012 were obtained from Fabra meteorological observatory, located in the Collserola Massif.

Finally, we used SADIE statistics (Perry and Hewitt 1991) with software SADIShell (Perry et al. 1999) to assess the spatial distribution of rodent abundance, acorn abundance and shrub cover along the study area, and their potential spatial association. We also performed analyses for males and females, and between the seed-rich seasons (autumn-winter) and the poor-seed seasons (spring-summer), since we did not have enough captures to assess the spatial patterns of mice for each single season. All mean values in the results are presented with their standard errors (mean \pm SE).

RESULTS

Throughout the 24 trapping sessions from June 2010 to July 2012, we captured 580 different individuals of *Apodemus sylvaticus* and two *Mus spretus*. The first 6 CMR models had more than the 90% of the weight (Table 2). The three first models were equivalent ($\Delta AICc < 2$), showing that: i) apparent survival probability varied mainly with the season, ii) the probabilities to emigrate (γ'') and to remain outside the trapping area (γ') differed with sex, and iii) capture and recapture probabilities varied with season and sex (Table 2).

Survival	γ''	γ'	Capture	Recapture	K	AICc	$\Delta AICc$	weight
Season	Site + Sex	Site + Sex	Season + Sex	Season + Sex	35	5169.28	0	0.33
Season + Site	Season + Sex	Site + Sex	Season + Sex	Season + Sex	43	5170.46	1.17	0.18
Season	Season + Sex	Site + Sex	Season + Sex	Season + Sex	42	5171.14	1.86	0.13
Season + Site	Site + Sex	Site + Sex	Season + Sex	Season + Sex	36	5171.37	2.09	0.12
Season + Sex	Site + Sex	Site + Sex	Season + Sex	Season + Sex	36	5171.4	2.12	0.12
Season + Sex	Season + Sex	Site + Sex	Season + Sex	Season + Sex	43	5173.28	4.00	0.04

Table 2. Models of CMR data with 90% of the weight and ordered according to the AIC. The models assess the effects of season, site and sex on the probabilities of survival, emigration from the study area (γ''), remaining outside the study area (γ'), capture, and recapture. The table also shows the number of parameters of the model (K).

The models revealed that seasonality largely affected the population dynamics of *A. sylvaticus*, whereas spatial variables had less effect: i.e. mice apparent survival probability, abundance, and body mass, were dramatically influenced by the season. Survival probability ranged from 0.36 ± 0.15 (summer of 2012) to 0.78 ± 0.08 (spring of 2012), with the lowest values registered during the three summers of the study period (Figure 1). Summer was also the season when rodents showed a lower body mass (Figure 2). The two summers with the lower survival likelihood (2010 and 2012) were also those with a more intense drought stress (drought index = 15.4 and 19.2 respectively). Accordingly, mice abundance (46.2 ± 5.3 individuals) showed strong seasonal variations, ranging from 8.0 ± 4.1 to 100.4 ± 5.4 individuals in the different trapping sessions, also with marked declines in the summers and rising again in autumn (Figure 3).

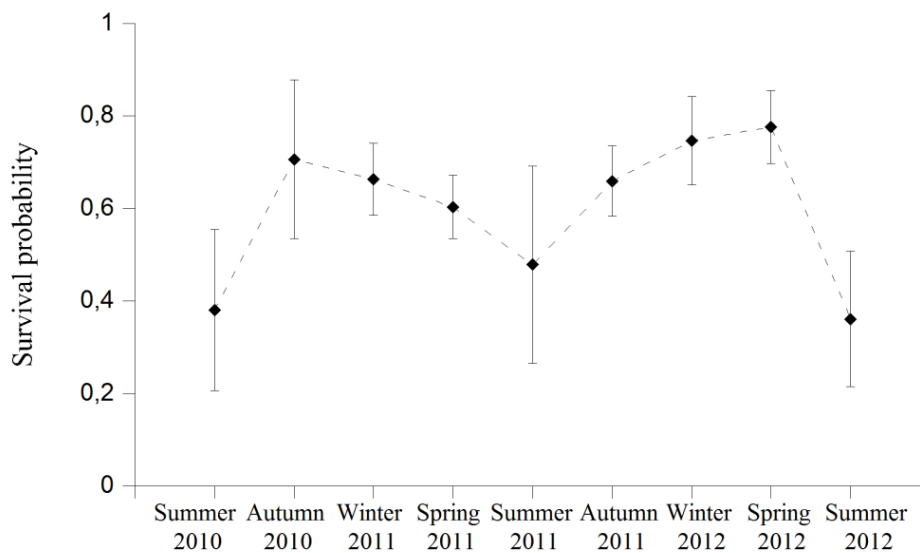


Figure 1. Model-averaged seasonal survival probability (mean \pm SE) of wood mice, according to the Huggins robust design models.

Besides seasonality, survival probability was not affected either by the wild boar enclosure (inside: 0.60 ± 0.12 ; outside: 0.59 ± 0.12) or by the sex (males: 0.60 ± 0.12 ; females: 0.60 ± 0.12). Similarly, we did not find any effects of the boar enclosure on the abundance of wood mice (inside: 21.7 ± 3.3 individuals; outside: 24.5 ± 4.0 individuals; $t_{22} = -1.59$, $p = 0.125$), or on their body mass (inside: 22.45 ± 0.24 g; outside: 22.45 ± 0.26 g; estimate = -0.03 ± 0.03 , CI = $-0.08, 0.03$). Concerning the effects of sex, female abundance along the different trapping sessions was generally higher (26.2 ± 3.6 individuals) than male abundance (20.0 ± 3.8 individuals; $t_{22} = 3.96$, $p < 0.001$), except in the summer periods, when mice population dropped

and the sex ratio was close to 50%. Conversely to the results of abundance, the probability of emigrating (γ'') and remaining outside the study area (γ') was slightly higher for males (0.60 ± 0.19 and 0.82 ± 0.09 respectively) than for females (0.48 ± 0.16 and 0.72 ± 0.11 respectively), but did not show any seasonal differences, or any effect of the enclosure treatment.

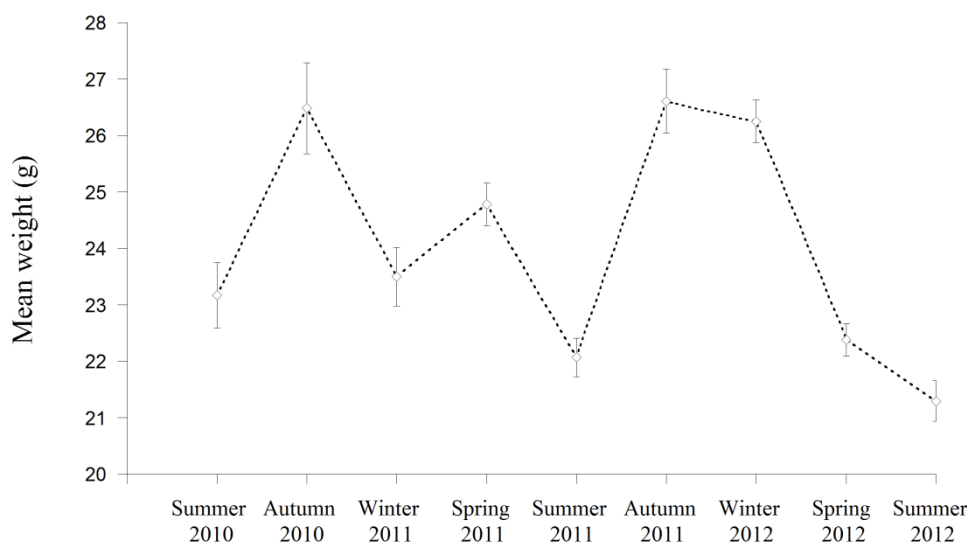


Figure 2. Weight variation (mean \pm SE) of wood mice according to the season for sub-adults and adults (excluding juveniles).

Summer season was the only period when no acorns were available on the ground in the Oak forest. In fact, acorn availability experienced drastic changes with season ($F_2 = 45.39$, $p < 0.001$), as acorns started dropping in autumn, achieved their greater abundance in winter (estimate = 2.68 ± 0.05 , $p < 0.001$) and became progressively scarce in spring (estimate = 1.95 ± 0.05 , $p < 0.001$) (Figure 3). Moreover, there were important interannual differences in the overall amount of acorns produced per year (sum of sound acorns from October to December), being twice higher in 2010 (88 acorns m^{-2}) than in 2011 (42 acorns m^{-2}). Interestingly, the seasonal changes of acorn abundance on the ground were positively correlated with the temporal changes in overall abundance of females ($F_{1,10} = 5.83$, $p = 0.036$), but not males ($F_{1,10} = 0.75$, $p = 0.406$).

Besides seasonal and annual changes, acorn abundance on the ground was lower outside ($2.9 \pm 0.7 \text{ acorns m}^{-2}$) than inside ($4.4 \pm 0.7 \text{ acorns m}^{-2}$) the wild boar enclosure (estimate = -2.10 ± 0.78 , $p = 0.007$). In that sense, it must be stressed that acorn abundance was quite randomly distributed in space in the two areas ($I_a = 1.19$, $p = 0.225$), and therefore it did not probably influence the spatial distribution of wood mice ($X = -0.20$, $p = 0.982$) at a fine scale (i.e. stake). In contrast, the spatial distribution of mice differed according to sex: females

showed a random spatial distribution ($I_a = 1.20$, $p = 0.216$), whereas males showed a strong aggregated pattern for the fall-winter period ($I_a = 2.26$, $p = 0.004$), but not for the spring-summer period ($I_a = 1.20$, $p = 0.092$). In any case, shrub cover had no effects on the spatial distribution of mice ($X = -0.05$, $p = 0.597$), or on the capture probability at each sampling point (estimate = 0.12 ± 0.22 , $p = 0.58$).

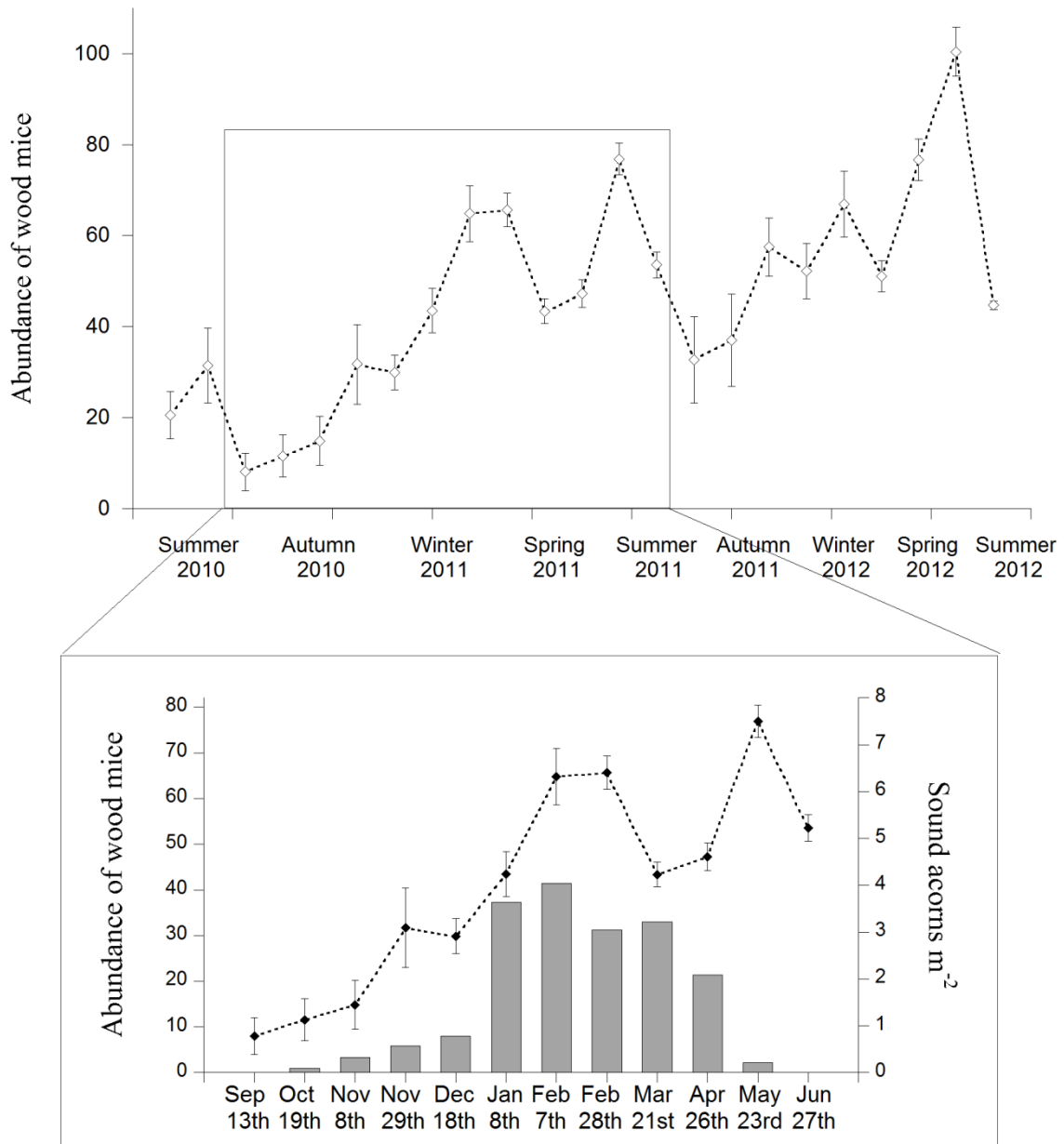


Figure 3. Model-averaged seasonal variations in wood mice abundance (number of wood mice in the study area \pm SE), according to the Huggins robust design models. The framed period also shows the temporal variation in acorn availability (sound acorns on the ground m^{-2}).

DISCUSSION

The demographic dynamics of *Apodemus* in our study area were strongly influenced by the seasonal variations in acorn abundance, and differed between males and females, supporting our initial hypotheses. Conversely, spatial patterns of mice did not match those of acorn abundance or shrub cover, and we did not find any influence of wild boars on the demographic parameters, therefore rejecting the other hypotheses.

In agreement with our first prediction, the dynamics of the mice population seem to be severely influenced by the season, as both mice survival and abundance experienced a marked drop in the three consecutive summers of the study period (Figures 1 and 3), also concurring with a decline in body mass during that season (Figure 2). The decline in abundance during the summer period matches with previous studies performed in other Mediterranean habitats (Rosário and Mathias 2004, Díaz et al. 2010), and differs from the dynamics described in central and northern Europe (Montgomery 1989a, b, Fernandez et al. 1996, Unnsteinsdottir and Hersteinsson 2011). Our results suggest that the high summer mortality is the main cause of the population decline in that season, since the emigration rates did not show seasonal variations. The strong summer decline most likely responds to the low food availability caused by the summer drought of Mediterranean environments (Herrera 1995, Torre et al. 2002, Rosário and Mathias 2004). In agreement we found that, on one hand, the body mass of mice decreased in the three summers monitored, and on other hand, the female abundance was closely related to the seasonal changes in acorn availability. Furthermore, the starting point of population growth of wood mice in autumn corresponded with the moment when oaks start dropping their acorns (Espelta et al. 2009a, Sunyer et al. 2014). Hence, albeit mice could use other less abundant food sources in our forest during summer (e.g. fruits from *Arbutus unedo* or pine cones from *Pinus halepensis*), acorns produced annually by oaks seem to have an overriding effect on their population dynamics. Moreover, it is unlikely that the high summer mortality is directly caused by a thermal and/or hydric stress, since our study area has a dense tree canopy and an abundant shrub understory, that provide shade and fresher conditions (Sunyer et al. in press; see also Schradin 2005, Muñoz et al. 2009, Rosalino et al. 2011).

In the summer of 2011, mouse abundance was higher due to a less severe reduction in survival (Figure 1), achieving higher densities by the end of spring (Figure 3). In fact, the summer drought of 2011 was less harsh due to an exceptionally high rainfall in June and July, which has been found to increase the availability of food for mice (i.e. herbs, insects and seed crops; see Díaz et al. 2010). In addition, this less stressful summer coincided with a particularly high acorn production the previous year (2010) that increased the overall availability of food for

mice. In such situations (e.g. mast years), rodent body condition may improve and female reproductive success (which is highly resource-dependent) may increase (Montgomery 1991, Rosário and Mathias 2004). In our oak forest, the higher acorn abundance led to a higher survival probability in summer, higher population recruitment in autumn-winter, and greater population abundance the following spring. Wood mice may scatter-hoard seeds which enable them to optimize their foraging strategies in situations of great food abundance, caching more acorns for further consumption in less favorable scenarios (Zhang et al. 2008, Vander Wall 2010). Similarly, many studies performed in northern Europe have also found that high food availability increase wood mice densities and overwinter survival, the season with adverse climatic conditions in northern Europe (Montgomery 1989a, Montgomery et al. 1991, Unnsteinsdottir and Hersteinsson 2011). Conversely, during the second year (2011-2012), while the abundance of mice was very high resulting from the previous acorn-rich year and wet summer, the production of acorns was much lower than the year before. We suggest that this high population density in spring combined with a low acorn availability probably increased the intraspecific competition, resulting in a drastic density-dependent regulation of the population (see Saitoh et al. 2008, Unnsteinsdottir and Hersteinsson 2011). These conditions could explain the strong population drop observed at the end of spring of 2012 (Figure 3).

As we anticipated in our third hypothesis, our results support sexual differences in the population patterns of wood mice. Females were randomly distributed along the study area, whereas males showed a more spatially aggregated pattern during the acorn fall seasons (autumn-winter). The different spatial distribution between males and females may probably respond to social interactions during the breeding season. In fact, autumn-winter is the main breeding period of wood mice in Mediterranean environments, when males have overlapping home ranges (Montgomery 1991, Fernandez et al. 1996, Godsall et al. 2014). Some studies have documented that females, but not males, spread out and maintain exclusive home ranges during the breeding season (Montgomery 1989b, Montgomery et al. 1991). In our study area, the random distribution in space of females and their lower mobility suggests that they display a more territorial behavior. Males, instead, travelled longer distances than females, probably seeking for mating opportunities across territories of different females, and thus increasing the probabilities of leaving the study area, as we have found with the CMR models (see also Torre et al. 2002, Rajska-Jurgiel 1992, Godsall et al. 2014). Notwithstanding these sexual differences in spatial distribution, the spatial patterns at a fine scale of either females or males were not influenced by the availability of acorns, probably due to the high density of oaks, that produce an overall homogeneous acorn shadows (see Espelta et al. 2009b). Surprisingly, we also found that the sex-ratio of the population was biased towards females, in contrast to the most common

findings previously reported (Montgomery 1989b, Montgomery et al. 1991, Fernandez et al. 1996, Rosário and Mathias 2004, Díaz et al. 2010), except in the summer when the entire population mostly collapsed. The match between seasonal changes in female abundance and acorn abundance, in an area with high seed crops might favor the establishment of many female exclusive territories and thus female-biased sex-ratios.

As in the case of acorn availability, the abundant and relatively continuous shrub cover (Sunyer et al. in press) probably explains the lack of matching between the spatial distribution of rodents and shrub cover at a fine spatial scale. The high tree and shrub densities of our oak forest contribute to ameliorate the thermal and hydric stress for *Apodemus* during the summer (Schradin 2005, Muñoz et al. 2009, Rosalino et al. 2011), but also provide a suitable microhabitat structure for protection against predators (Schradin 2005, Perea et al. 2011b, Rosalino et al. 2011). Besides protecting against predators, shrubs can also attenuate the effects of large ungulates on rodents (Muñoz et al. 2009). For example, dense shrubs can serve as protected areas from wild boar rooting activity, direct trampling and soil compaction, which seem to represent more serious threats for the biology of *Apodemus* than the competition for acorns (Focardi et al. 2000, Smit et al. 2001, Daniel et al. 2002, Muñoz et al. 2009). Hence, although wild boars reduced acorn availability on the ground, we did not find any significant impact on the population of wood mice in our oak forest. This lack of effect contrasts with other studies carried out in open habitats that have reported reductions in rodent's abundance of up to 80% (Muñoz et al. 2009), revealing the importance of the habitat characteristics in mediating the effects from big ungulates. Additionally, even though wild boars had no effects on wood mouse demographic dynamics, they might have a strong influence in the behavior of rodents and their foraging decisions (Muñoz and Bonal 2007). Indeed, Sunyer et al. (in press) found in the same experimental area that wild boars modified the seed dispersal/predation behavior of wood mice, since in those places rooted by boars, rodents reduced the dispersal rates of acorns and increased their consumption *in situ*.

In summary, we have shown that wood mice in Mediterranean oak forests can be constrained by several environmental factors, and that acorn availability seems to be the main one ruling their population dynamics. Several studies have addressed the role of wood mice, and other acorn-dispersing rodents, on the recruitment of oaks (see among others Pulido and Díaz 2005, Gómez et al. 2008, Perea et al. 2011a). However, there is comparatively little information on how oaks (i.e. acorn crops) can condition the population dynamics of their rodent dispersers (see Shimada and Saitoh 2006 for a review). Our study highlights that the relationships between acorn dispersers and oaks can be more reciprocal than previously considered. On other hand, spatial microhabitat features such as wild boar presence, shrub cover, and the distribution of

acorns were less significant in our study area, probably due to the continuous canopy cover, high shrub densities, and high acorn production of these forests. These results contrast with the patterns observed in more sparse oak forests in drier environments (e.g. Muñoz et al. 2009, Perea et al. 2011b, Rosalino et al. 2011), highlighting the importance of contextual differences among different sites (even among oak forests). Hence, we suggest that further studies assessing the relative importance of environmental and intrinsic factors on the regulation of rodent's populations would benefit by considering the importance of the context when extracting general conclusions.

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CHAPTER 2

Seeding phenology influences wood mouse seed choices: the overlooked role of timing in the foraging decisions by seed-dispersing rodents

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SUMMARY

Scatter-hoarding rodents influence the population dynamics of plants by acting as seed predators and dispersers. Therefore, rodents' foraging preferences for certain seed traits (species, size, condition) have been extensively studied. However, to what extent these preferences are fixed or they track the temporal changes on seed characteristics due to phenological differences, has been seldom explored. We studied the temporal variability in seed preferences by wood mouse (*Apodemus sylvaticus*), according to phenological changes in seed characteristics of two co-occurring oaks (*Quercus ilex* and *Q. pubescens*). The phenology of acorn abundance and the acorn predation/dispersal patterns by rodents were monitored over an entire seeding season. Results revealed temporal changes in rodents' preferences for acorns of the two oaks, matching their different seeding phenology (earlier in *Q. pubescens*, later in *Q. ilex*). On the other hand, whatever the species considered, rodents preferred larger and sound acorns along the entire season, although the dispersal of infested ones increased slightly during the peaks of acorn drop. The observed influence of seeding phenology on seed choices by rodents warns about inferring definite conclusions regarding their foraging behavior when arising from short-term experiments. Indeed, this study reveals that foraging preferences may be highly dynamic and context-dependent for some seed traits (e.g. species, condition), rather than fixed behavioral patterns. Plasticity in rodents' foraging choices may allow them to successfully exploit different oaks with uncoupled seeding phenologies, while potentially favoring their coexistence.

Key words: Acorn; *Apodemus sylvaticus*; *Quercus*; Seed dispersal; Seed traits

INTRODUCTION

Scatter-hoarding rodents strongly influence the population dynamics of many plant species due to their dual role as seed predators and dispersers (Vander Wall 1990, Hollander and Vander Wall 2004). Indeed, the foraging decisions and preferences of rodents may ultimately determine the fate of seeds, thus influencing the reproductive success and life-history traits of plants (Janzen 1970, Vander Wall et al. 2005, Beck and Vander Wall 2010, Vander Wall 2010, Sivy et al. 2011, Muñoz et al. 2012). For this reason, many studies have analyzed the foraging behavior of granivorous rodents, for the most part testing their responses to different seed traits such as species, seed size, shape or condition (e.g. Shimada 2001, Vander Wall 2001, Jansen et al. 2004, Heredia and Detrain 2005, Moore et al. 2007, Zhang et al. 2008). Species may influence seed choice by rodents due to interspecific differences in seed physical characteristics (e.g. hull thickness) or chemical composition (e.g. tannins content) (see Pons and Pausas 2007, Sivy et al. 2011, Xiao et al. 2013a). With seed size, larger seeds are usually dispersed over longer distances and preferentially cached as opposed to small ones, which are more likely to be predated *in situ* or dispersed closer to the seed source (Jansen et al. 2002, Xiao et al. 2005, Muñoz and Bonal 2008a, Wang and Chen 2009, Xiao et al. 2013b). In addition, seed condition (i.e. sound or parasitized) may also influence seed fate as rodents often avoid rotten seeds or those infested by insect larvae (Muñoz and Bonal 2008b, Perea et al. 2012a).

Although certain seed characteristics may play by themselves an overriding effect on seed choice by rodents, it would be more realistic to consider their potential interaction with other seed traits or the context in which decisions are taken (e.g. the relevance of seed abundance in Xiao et al. 2010, the interaction among seed size and germination in Xiao et al. 2013b). Indeed, seed abundance (crop size) is also known to shape the foraging preferences of seed-dispersing rodents, for example, by altering the balance between seed predation and caching (Vander Wall 2002, Jansen et al. 2004, Saitoh et al. 2008, Zhang et al. 2008, Xiao et al. 2013a, c). These studies have documented changes in the patterns of seed predation and dispersal between mast and lean years, suggesting that rodents can adapt their decisions to temporal changes in seed availability. However, seed abundance may be extremely variable not only among years but also within the same year. Owing to phenological differences, both between and within species, intense and poor seed fall peaks occur at different moments throughout the seeding season (Bonal and Muñoz 2007, Espelta et al. 2009a). Moreover, temporal variability may be not only quantitative, but also qualitative, as the characteristics of the seeds available for rodents may change throughout the season. In mixed oak forests, for example, inter-specific discordances in flowering phenology of the co-occurring species may cause large temporal differences in the availability of seeds for rodents (e.g. deciduous vs.

perennial oaks in Fernández-Martínez et al. 2012, see also Lichti et al. 2014). In addition, insect phenology can also make the number of infested and sound seeds available vary greatly throughout the season (Bonal and Muñoz 2007, Espelta et al. 2009a). Nonetheless, since most studies analyzing rodent preferences have focused on specific seed traits, or have been conducted at a single time, the relevance of phenological differences over the same seeding season has hardly been specifically considered, and remains as part of the unexplained variability. Moreover, the inclusion of phenological trends can also shed light on the potential effects that changes in the phenology of seed production, mediated by climate change (e.g. Sánchez-Humanes and Espelta 2011), may have on rodent behavior and other cascading effects on upper trophic levels.

To evaluate to what extent seeding phenology may influence rodents seed choices we have analyzed the temporal variability in the foraging behavior of scatter-hoarding rodents throughout a seeding season according to the changes in seed characteristics (species, size and condition) and seed abundance using a mixed Mediterranean oak forest (*Quercus ilex* and *Q. pubescens*) as a model system. This is an interesting model for addressing this question for several reasons. First, oak forests are an excellent habitat for the wood mouse (*Apodemus sylvaticus*), one of the main acorn predator/disperser for both oak species, as acorns constitute the bulk of rodent diet during the seeding season (Perea et al. 2011, Sunyer et al. 2013). Second, both oak species differ in the timing of flowering and acorn growth (Fernández-Martínez et al. 2012) and thus, both suffer different infestation rates by weevil (*Curculio* spp.) larvae (Espelta et al. 2008), which attack their acorns at different times of the season (Espelta et al. 2009a).

Our main objective was to unravel how the different phenologies of seeding in *Q. pubescens* and *Q. ilex*, as well as acorn infestation timing might influence the acorn preferences of the wood mouse and, ultimately, acorn predation and dispersal patterns. Specifically, we assessed whether rodents showed a fixed foraging preference towards some particular seed traits (species, size, condition) throughout the entire seeding season or, by contrast, they modified these preferences according to the phenological changes in the availability of the different acorn types. We hypothesize that, rather than exhibiting a fixed foraging behavior, rodents will change their preferences according to: i) changes in the availability of acorns from each oak species, ii) variations in the total abundance of acorns and iii) changes in the proportion of infested and sound acorns. If seed preferences are driven by phenological changes within the same seeding season, then rodents' decisions should be viewed as a highly dynamic and mutable process with important implications for the ecology of seed dispersal (Sunyer et al. 2013).

METHODS

Experimental Design

Phenology of acorn and wood mouse abundances

Throughout the entire seeding season of 2010-2011 we monitored the phenology of acorn abundance of the two oak species in the study area by placing four seed traps (i.e. buckets with a 38-cm diameter) under 40 different adult trees (20 *Q. ilex* and 20 *Q. pubescens*) with a similar crown size (for a similar procedure see Bonal and Muñoz 2007). Traps were installed in early summer, before the seeding season started. Periodically (*ca.* 15 days), we checked the seed traps and counted the number of acorns per tree distinguishing between infested (identified by the characteristic mark left by the oviposition and kept apart until the emergence of the larva) and sound ones until the seeding season finished (i.e. all acorns had dropped from these focal trees). This allowed us to calculate an estimate of the number of acorns (total, infested, sound) dropped per tree (acorns m⁻²) in each sampling over the entire seeding season. Two species of acorn weevils are present in the study area (*Curculio glandium* and *C. elephas*) that oviposit into the acorns while these are still growing (Espelta et al. 2009a). Acorns are prematurely abscised after being attacked and larvae continue their development consuming the cotyledons within the dropped acorns (Bonal and Muñoz 2009). The impact of weevils on acorns is higher at the beginning of autumn, and thus *Q. pubescens* often suffers higher rates of predation by weevil larvae as their acorns develop earlier (Espelta et al. 2008). Once collected, we measured the volume of every acorn as a proxy of its size. We measured volume rather than weight because the weight of weevil infested acorns may be extremely variable depending on how much cotyledons larvae have already chewed (Bonal and Muñoz 2007).

To monitor phenological variations in rodent abundance we performed monthly trapping campaigns with standard Sherman live-traps (23.5 x 8 x 9 cm; HB Sherman Traps Inc. Tallahassee, Florida USA) throughout the entire seeding season. In every campaign we placed 132 Sherman traps baited with a mixture of flour and tuna in oil, and a piece of apple as a reward and to avoid dehydration. Additionally all the traps also contained a handful of hydrophobic cotton so that the captured rodents could make a nest to keep warm until they were marked and released (Muñoz et al. 2009). The traps were set for four consecutive nights at sunset (i.e. 20:00 hours GMT) and were checked every morning at sunrise (i.e. 07:00 hours GMT). Every campaign the traps were placed in the exact same locations, which were marked with wooden sticks, forming a grid with a 10-meter separation between traps along the study area. Captured rodents were permanently marked using microchips (MUSICC, AVID Identification Systems Inc.; size = 8 mm; weight = 0.06 g) implanted under the skin below the

neck, which allowed us to individually identify each recaptured rodent. The chip was implanted without surgery, using a specialized syringe (AVID SUDS monoject), afterwards it was massaged away from the point of insertion (Sikes et al. 2011) and iodine was applied to the punctuation wound to prevent any infection. Once marked, all captured animals were released at the exact same point where they were caught. Throughout the entire season we captured 156 different individuals of *Apodemus sylvaticus* and only three of Algerian mouse (*Mus spretus*) over the eight trapping campaigns.

Phenology of acorn predation and dispersal by rodents

At the same site where acorn and rodent abundances were measured, we also monitored the patterns of predation and dispersal of acorns during the whole season. We collected and weighed ripe acorns of both oak species from the ground and monitored their fate (predation or dispersal by wood mice) by attaching a 40-cm-long wire with a bright purple flagging tape on which an alphanumeric code was written. This method makes it possible to locate the dispersed seeds and does not influence seed dispersal behavior by rodents (Xiao et al. 2006, Yang et al. 2012). Other potential side-effects of this method (pilferage rates increase) would not affect our results on phenological changes in seed preferences, since all acorns were marked in the same way through the seeding season. We randomly placed 40 seed stations over the study area, each consisting of a feeding plot protected by a 40x40x20 cm wire cage with a mesh size of 5x5 cm in which the marked acorns were placed, ensuring that only scatter-hoarding rodents would have access to them (Muñoz and Bonal 2007, 2011, Sunyer et al. 2013). We placed 320 tagged acorns along the 40 sites so that each feeding plot had eight acorns: four acorns per species (*Q. pubescens*, *Q. ilex*), two infested by weevil (not containing the larva) and two sound ones. Acorns of *Q. pubescens* were heavier than those of *Q. ilex* (Mean weight \pm SE respectively = 1.64 ± 0.05 g and 1.11 ± 0.03 g), and sound acorns were heavier than those infested (Mean weight \pm SE respectively = 1.34 ± 0.04 g and 1.00 ± 0.03 g). From the beginning to the end of the seeding season, and on a *ca.* two-three week basis, we revised the seeding stations for monitoring acorn preferences by rodents. We recorded the acorns predated *in situ* and those dispersed (moved outside the cage). Dispersed acorns were tracked and their species, dispersal distance (distance from the edge of the cage), fate (predated or intact) and type of microhabitat where it was found (open/shrub) were recorded. For the purposes of this study, partially consumed acorns were considered as predated. Whether the acorns were finally able to germinate or not is something out of the scope of this study, as the choices made by the seed-dispersing rodent are the same regardless of the final seed fate. At each revisited we replaced all the acorns (used and not used by rodents) from every seed station with new fresh ones collected on the ground, maintaining the same proportion of species (*Q. pubescens*, *Q. ilex*) and acorn

condition (sound or infested) at each seeding station. Thus, by the end of the study we had monitored the fate of 2560 acorns (= 320 acorns x 8 revisits). Acorns that were dispersed but not eaten were left on the field and revised during the following samplings, until they were predated or redispersed to a new location.

Data Analysis

The differences in the phenology over the season of acorn drop (total, infested, sound) and acorn size between species, as well as the patterns of acorn condition (infested or sound) within each species were analyzed by means of repeated measures ANOVA tests, where “species” or “condition” were the between-subject factors, respectively, and “date” was the within-subject factor. We also performed a LS-means test to determine the statistical differences among the levels of the categorical factors.

Generalized linear mixed models (GLM) and general linear mixed models (GLMM) were used to analyze the patterns of acorn use by rodents. We used GLM, with a binomial error distribution to analyze the effect of species (*Q. ilex*, *Q. pubescens*), acorn condition (infested, sound), abundance of acorns per sampling (dropped acorns m⁻²) and rodent abundance (number of individuals of *A. sylvaticus* captured per sampling) on the decision of rodents to manipulate an acorn or not (manipulation model) and the decision to predate it *in situ* or disperse it (dispersal model). We also ran a GLM with a binomial error distribution and a logit link function for specifically assessing the effect of the sampling date (categorical, from 1 to 8) on the proportion of dispersed acorns of *Q. ilex* and *Q. pubescens* to test for temporal differences on species preferences by rodents. A type II test was performed to obtain a p-value for the categorical factor, and a general linear hypothesis test to determine the significant differences among the levels of the categorical factor. We used GLMM to analyze the effect of species, acorn condition, acorn weight, abundance of acorns per sampling, rodent abundance, and the sampling date on the dispersal distance of acorns (distance model). In all GLM and GLMM models the seed station (sites were seed where placed) was included as a random factor to check for spatial variability. In addition to the analyses of the timing in acorn dispersal, we also performed a chi-square test to determine whether rodents preferred to manipulate a particular oak species over the entire season. The statistical analyses presented were performed with STATISTICA (Weiss 2007) and R (R Development Core Team 2008).

This study was conducted in accordance to the current Spanish legislation and with a permit of the Collserola Natural Park authorities to conduct this study (Num: 808).

RESULTS

Phenology of Acorn Abundance

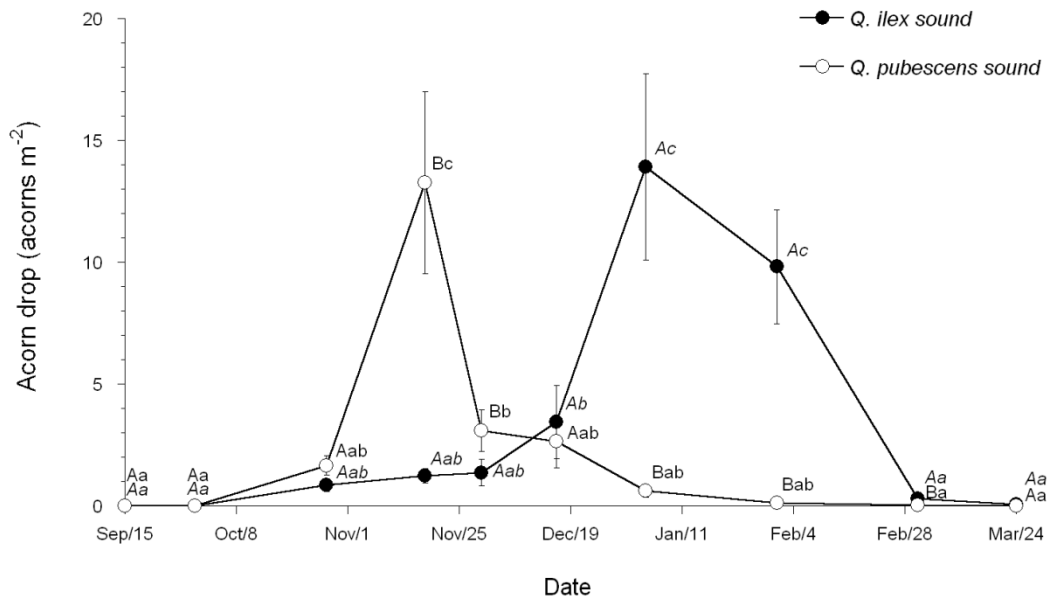
As expected, the acorn abundance phenologies of the two oak species were not coincident in time, as *Q. pubescens* acorns dropped significantly earlier than *Q. ilex* ones (Date*Species $F_{9,342} = 10.76$, $p < 0.001$). The earlier phenology of *Q. pubescens* (relative to *Q. ilex*) also resulted true when considering the drop of sound acorns and the drop of infested acorns separately (respectively, $F_{7,266} = 13.31$, $p < 0.001$ and $F_{9,342} = 3.63$, $p < 0.001$, Figure 1). At a within species level, in both oaks infested acorns dropped earlier than sound ones (Date*acorn condition; *Q. pubescens*: $F_{7,266} = 3.87$, $p < 0.001$ and *Q. ilex*: $F_{9,342} = 11.79$, $p < 0.001$). Acorn size also differed between the two oaks: i.e. acorns of *Q. pubescens* were significantly larger ($2.12 \pm 0.03 \text{ cm}^3$) than those of *Q. ilex* ($1.62 \pm 0.02 \text{ cm}^3$; $F_{4,24} = 4.46$, $p = 0.008$) and this difference held true when analyzing sound and infested acorns separately (respectively, $F_{4,16} = 6.30$, $p = 0.003$; $F_{3,18} = 11.94$, $p < 0.001$).

Phenology of Acorn Preferences by Rodents

Acorn manipulation, either predation *in situ* or dispersal was highly influenced by acorn size ($\beta = 0.62 \pm 0.14$, $p < 0.001$) and acorn condition ($\beta = 4.15 \pm 0.51$, $p < 0.001$), so that rodents tended to preferentially manipulate larger and sound acorns (76 % in *Q. pubescens* and 88 % in *Q. ilex*). Nonetheless, the interaction between acorn condition and size (acorn condition*size $\beta = -0.81 \pm 0.17$, $p < 0.001$) indicated that rodents tended to manipulate sound seeds of intermediate sizes, but selected the larger acorns among the infested ones. Interestingly, the negative effect of infestation on the likelihood of acorn manipulation was also dependent on the phenology of acorn abundance as it increased slightly during the peaks of acorn fall (interaction acorn condition*acorn fall m^2 , $\beta = -0.20 \pm 0.06$, $p < 0.001$), even though the amount of infested acorns manipulated was very low throughout the season.

Rodents behaved mainly as acorn dispersers rather than as predators since, on average, they dispersed 89 % of sound acorns and only predated 11 % *in situ*. This behavior was quite constant over the entire seeding season (Figure 2). However, the majority of the dispersed acorns (91 %) were ultimately predated after dispersal. The decision to remove or predate an acorn *in situ* mainly depended on acorn size ($\beta = 0.48 \pm 0.23$, $p = 0.04$), whatever the acorn condition (sound or infested), with the larger acorns being the ones preferentially dispersed. Dispersal distances ranged from 0.05 m to 15 m (mean \pm SE, 1.4 ± 0.2 m; $n = 123$) and were not affected either by acorn species, acorn weight, or by the sampling date (type II test $\chi^2_7 = 12.33$, $p = 0.09$). Most dispersed acorns were moved to “safe” microhabitats (e.g. under bushes or in burrows), as only 17 % were found un-buried in an open microhabitat.

a) Sound acorns



b) Infested acorns

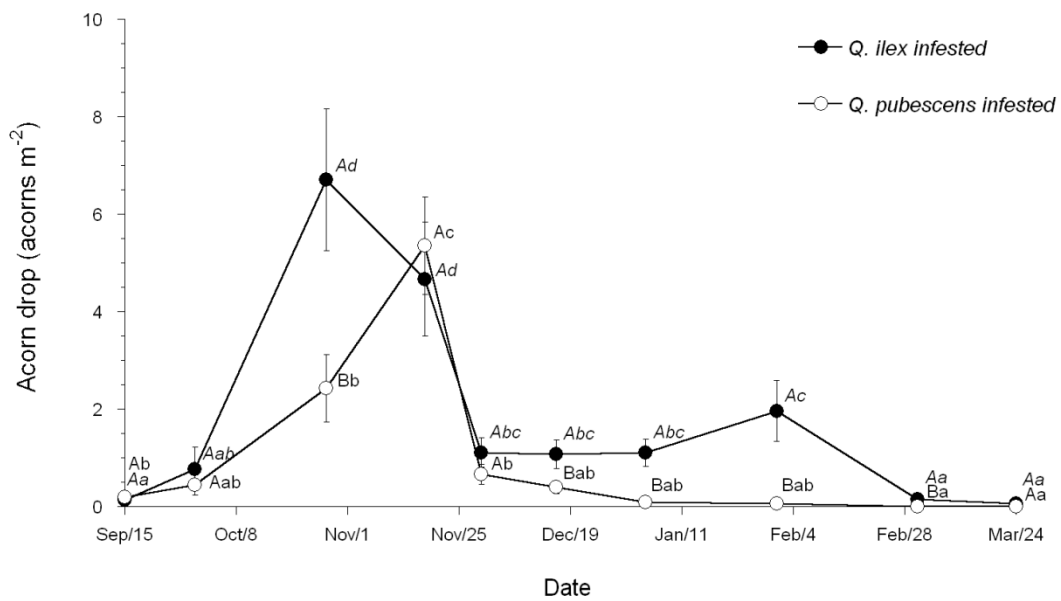


Figure 1 Mean \pm SE of sound (A) and infested (B) acorns dropped per oak species (*Q. ilex* and *Q. pubescens*) along the entire seeding season. Different letters (in italics for *Q. ilex*) indicate significant differences between both species (upper case letters) and among the different dates within the same species (lower case letters), according to the LS means test

Rodents apparently did not show preferences for dispersing *Q. pubescens* or *Q. ilex* acorns when considering the overall number of acorns dispersed during the entire seeding season (respectively, 53 % vs. 47 %; $\chi^2_1 = 0.45$, $p = 0.504$). However, this apparent lack of preferences changed dramatically when considering the timing of acorn dispersal, since rodents changed radically their preference for each oak species over the season (Type II test $\chi^2_7 = 21.12$, $p = 0.004$). At the beginning, they preferred to remove *Q. pubescens* acorns while, at the end of the season, they preferred *Q. ilex* ones (Figure 3, dispersal preference). This uncoupled pattern of acorn preferences between the two oak species seemed to be related to the phenology of acorn abundance (earlier in *Q. pubescens* than in *Q. ilex*). In fact, the temporal pattern of rodent preferences for a particular species matches the temporal pattern of acorn fall for that species, but with a delay of *ca.* one month (Figure 3).

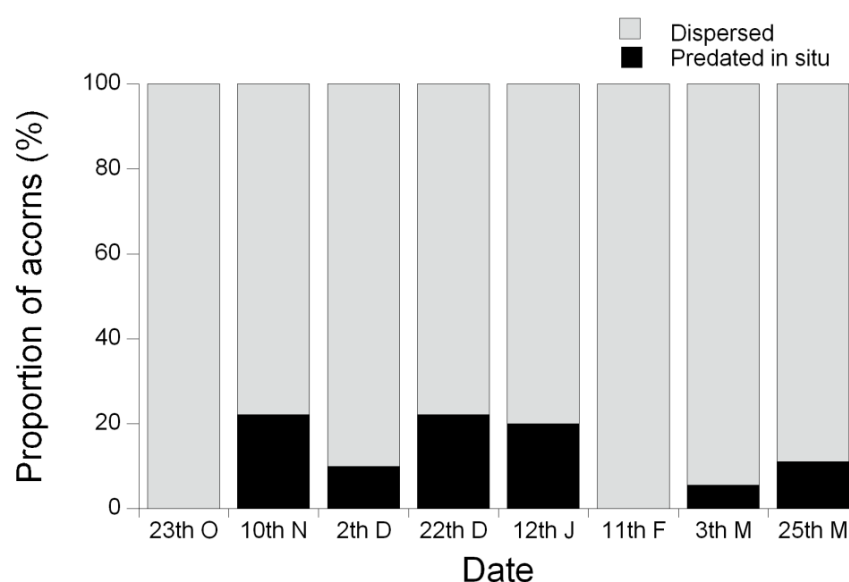


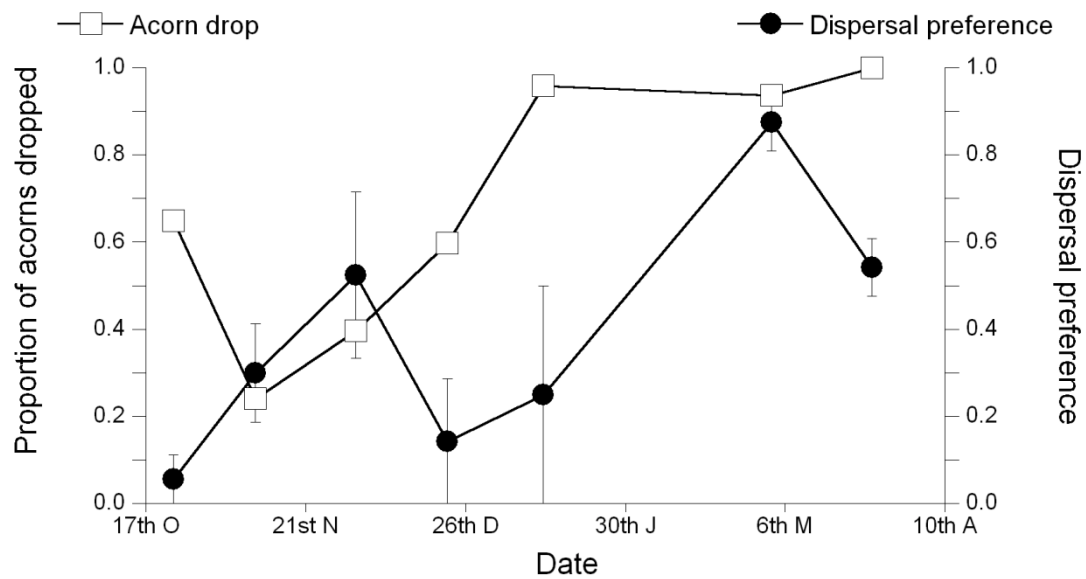
Figure 2 Proportion of sound acorns (%) dispersed or predated *in situ* by rodents along the seeding season

DISCUSSION

This study reveals the existence of significant changes over the seeding season in the preferences of scatter-hoarding rodents for certain seed traits, like species and seed condition, driven by phenological differences between two co-occurring oaks. This warns us about inferring general rules about rodent preferences arising from very short-term experiments, since they could lead to biased predictions. For example, if a study had been conducted just in December in our study area it would have concluded that rodents preferred to disperse *Q.*

pubescens acorns over *Q. ilex* ones, while, if performed in February it would have claimed the opposite behavior. However, when considering the entire season, the proportion of acorns dispersed from each species at the end of the seeding season was very similar (53 % in *Q. pubescens* vs. 47 % in *Q. ilex*). Conversely, rodent's behavior was more regular in removing larger acorns over the whole season, which indicates that selection for a larger seed size is a more fixed preference in mice.

a) *Q. ilex*



b) *Q. pubescens*

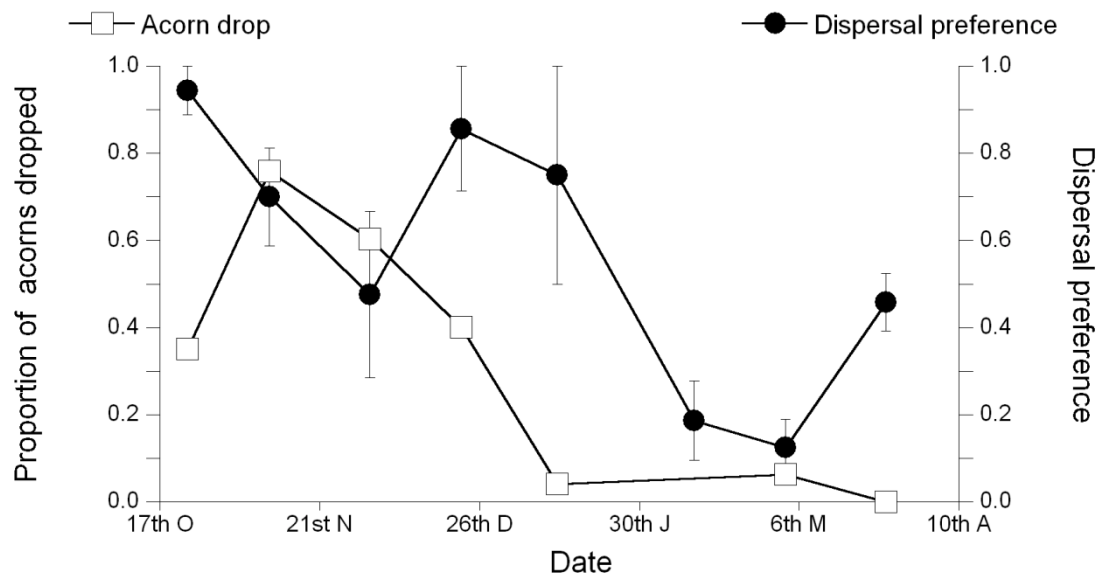


Figure 3 Mean \pm SE proportion of acorns dropped and dispersal preference for *Q. ilex* (A) and *Q. pubescens* (B) considering the acorns of the two species

Studies with other seed dispersers, have documented how their ability to track tree fruits, a spatiotemporally variable resource, may cause foraging changes in accordance to the changing availability and species composition of their resources (see for birds: García and Ortiz-Pulido 2004, Richardson et al. 2013, and for other rodents Xiao et al. 2013a, Lichti et al. 2014). In line with these studies, it is highly probable that the clear changes in the preferences of the wood mouse for the acorns of one oak species or the other resulted from the inter-specific differences in acorn drop phenology. Since at our seed stations we always placed the same number of fresh acorns of both species, these results suggest that rodents foraging behavior is plastic, changing their preferences in accordance to the most available food resource at a given moment.

Interestingly, rodent decisions have been claimed to be framed within optimal foraging models, which predict that food intake should be maximized and foraging costs reduced (Jorge et al. 2012). This is probably the reason why over the seeding season mice searched for the dominant acorn species, as it would be too costly – and probably dangerous – to search constantly for a specific species (e.g., the more nutritious *Q. ilex*) when this species is barely present on the forest floor (see also Muñoz and Bonal 2008b). Moreover, although some synchrony has been observed between acorn crop size in *Q. ilex* and *Q. pubescens*, there is a huge inter-annual variability (Espelta et al. 2008). Thus, a rather fixed preference for a particular oak could be negative, as poor years of this species may coincide with an abundant crop of the other (for these two oaks, see Fernández-Martínez et al. 2012). These changes during the season may help to explain why some short term studies have argued for a positive selection of some particular oak species by wood mice (Pons and Pausas 2007) while others did not find any preference at all (Espelta et al. 2009b). The uncoupled phenologies of the two oak species, coupled with the lack of preferences of rodents for a particular one, may provide a window of chance for seed dispersal of both species, ultimately assisting their coexistence (see also Espelta et al. 2009b).

In contrast to the plasticity in species preferences we found a more fixed behavior throughout the season concerning acorn condition and size: i.e. a preferential selection of sound acorns or larger ones if infested by weevil. Rejection of weevil infested acorns by rodents is often interpreted as a mechanism to avoid investing time in seeds in which cotyledons have been mostly depleted by larvae (Steele et al. 1996, Muñoz and Bonal 2008b), although some studies have documented that infested acorns with the larvae still inside can be also predated *in situ* (Perea et al. 2012b). Indeed, seed size has been recognized to be of paramount importance in seed choice by granivorous animals and a myriad of studies have reported the marked preference of rodents for removing larger acorns (Vander Wall 2001, Jansen et al. 2002, 2004,

Xiao et al. 2005, Wang and Chen 2009), a decision that may have dramatic consequences for the fate of seeds: i.e. predation *in situ* of the smaller ones while dispersing and caching the larger ones (Theimer 2003, Jansen et al. 2004, Xiao et al. 2005, Rush et al. 2013). The fact that the very few infested acorns manipulated and dispersed in this study were the larger ones: i.e. those that might still offer some nutritional reward, reinforces this importance of seed size. Nevertheless, the slight increase in the use of weevil infested acorns during the peaks of acorn drop also highlights the context-dependent plasticity of rodent foraging preferences concerning acorn condition.

Despite the variability in acorn availability and the changes in rodent foraging choices throughout the season, the patterns of acorn predation vs. dispersal remained quite constant (see Figure 2). The fact that rodents dispersed the vast majority of the acorns they manipulated suggests that they initially acted predominantly as potential seed dispersers (see Sunyer et al. 2013 for similar results), although most of the dispersed acorns were predated afterwards. Unfortunately, we were not able to elucidate whether the dispersed acorns were predated by the mice that cached them or by pilferers. The increase in the size of the population of rodents in our study site along the season, coupled with some previous results in the literature, suggests that pilferage rates may be extremely high (for a review, see Vander Wall and Jenkins 2003). Moreover, we cannot discard that the flag-tagging method we used could account in part for the high predation rate of removed acorns, as it adds a visual mark to the acorns making them more conspicuous.

The plasticity of wood mice in their foraging decisions described in this study may have significant implications for understanding the ecology of seed dispersal and the evolution of this plant-animal interaction. First, our results contribute to highlight that short-term changes in rodent behavior may be strongly context-dependent for some seed traits but not for others. This suggests some caution when considering the role of single traits on rodent decisions and the hypothetical selective pressures exerted by them. Similarly, the fact that even the effect of seed condition varied throughout the season questions the paramount relevance attributed to these traits in terms of seed successful recruitment. Finally, a challenging issue will be to address how climate change might alter this plant-animal interaction by changing flowering and seeding phenologies (for these oak species, see Fernández-Martínez et al. 2012, for other species, Peñuelas et al. 2002), resulting in a potential mismatch between plant phenology and rodent activity.

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CHAPTER 3

The ecology of seed dispersal by small rodents: a role for predator and conspecific scents

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SUMMARY

Seed-caching rodents play a key role in the ecology of seed dispersal by not only consuming but also dispersing seeds. Rodent foraging behaviour is usually framed within optimal models, which predict that their decisions should maximize food intake and minimize foraging costs. Yet, although predation risk and seed pilferage by conspecifics have been envisaged as two potential costs, their relevance for seed-caching behaviour and seed dispersal has barely been addressed. To test the effect of predation and pilferage risk on the patterns of seed predation/dispersal by rodents, we performed a field experiment using a tri-trophic-level model (plant-mice-carnivore; *Quercus* spp-*Apodemus sylvaticus*-*Genetta genetta*,) and the scents of the predator and conspecifics as direct cues. The behaviour of mice was analyzed with video cameras set for continuous recording on consecutive nights and we used tagged acorns to assess the patterns of acorn predation and dispersal. Our results revealed that rodents were able to discriminate between the scents of genet and conspecifics and modified their seed dispersal behaviour accordingly. Mice spent more time “sniffing” in rodent cages than in genet cages, where they displayed more “vigilance and freezing” behaviours. In sites with mice scents, acorns were dispersed at shorter distances and were less predated. Conversely, in sites with genet scents acorn removal was delayed. These results show that chemosensory information on predators and conspecifics influences the foraging decisions of seed-caching rodents over short spatial and temporal scales. This might entail cascading effects on the regeneration of plants. In sites where rodents perceive the risk of predation, inefficient foraging behaviour may result in less successful seed dispersal. Conversely, the detection of conspecific scents may increase dispersal efficiency and seedling recruitment. Ultimately, the relationships between two distant levels in trophic webs (plants-carnivores) appear intricate, since carnivores may affect seed dispersal by changing the foraging behaviour of their prey (the seed disperser). This indirect relationship should be considered as a new dimension of the ecology of seed dispersal by small rodents.

Key words: *Apodemus sylvaticus*; *Quercus* spp.; trophic webs; odour cues; acorn; genet

INTRODUCTION

Many small rodent species act as prominent seed dispersers by moving and caching seeds that may not be recovered and thus germinate (Vander Wall 1990, Hollander and Vander Wall 2004). This process may have strong effects on seed dispersal patterns and the recruitment dynamics of many plant species (Den Ouden et al. 2005, Xiao et al. 2005). Hence, the study of foraging decisions by rodents is fundamental to understanding seed dispersal and plant regeneration dynamics (Cousens et al. 2010, Muñoz and Bonal 2011). The foraging decisions of seed-caching rodents consist of a set of sequential choices that determine seed fate: basically, whether the seed is consumed immediately or transported and cached at a certain distance in a given microhabitat (Vander Wall 1990, Muñoz and Bonal 2011). Many factors are known to influence rodents' choices through this decision-making process, such as seed traits (e.g. seed size, seed infestation by insects, seed species (Steele et al. 1996, Jansen et al. 2002, Pons and Pausas 2007, Muñoz and Bonal 2008a), seed abundance (Shimada and Saitoh 2006), the presence of ungulates (Muñoz and Bonal 2007), microhabitat structure (Muñoz and Bonal 2011, Perea et al. 2011a, Perea et al. 2011b), and even rodents' previous foraging experience (Muñoz and Bonal 2008a).

Rodents' decisions are usually framed within optimal foraging models where decisions should maximize food intake and reduce foraging costs (Lima and Dill 1990, Brown and Kotler 2004, Jorge et al. 2012). In this scenario, it is well documented that predation risk is a key foraging cost for small rodents (Sih 1980, Lima and Dill 1990, Brown et al. 1999) given that they are at the base of many trophic webs and so are a common prey of a wide array of terrestrial and aerial predators (Jedrzejewski et al. 1993, Taraborelli et al. 2008). In addition, the pilferage risk of cached seeds by conspecifics may also represent an important foraging cost in the case of scatter-hoarding rodents (Vander Wall and Jenkins 2003, Dally et al. 2006). Both predation risk and pilferage risk are known to interact and change according to habitat features, so that microhabitats with low predation risk can also have higher rodent densities, thus increasing competition for food (Sih 1980, Kotler et al. 1991, Manson and Stiles 1998). For example, in Mediterranean oak woodlands, shrubs reduce predation risk for small rodents but also increase the risk of seed pilferage, because rodents are usually concentrated under shrubs (Muñoz and Bonal 2007, Muñoz et al. 2009, Muñoz and Bonal 2011). This makes it difficult to disentangle the individual effects of perceived predation and pilferage risk on rodent foraging decisions. Thus, to shed light on this issue it is necessary to rely on direct cues, which is to say unequivocal indicators of predator or conspecific presence managed by rodents in order to balance their foraging costs (Kats and Dill 1998, Brown and Kotler 2004, Orrock et al. 2004).

Direct cues of predator presence, especially in nocturnal rodents, are mostly gathered via olfaction (Jedrzejewski et al. 1993, Herman and Valone 2000). In fact, rodents show an extraordinary olfactory sensitivity that enables them to respond to predator scents (Nolte et al. 1994, Takahashi et al. 2005) and even discriminate among different predators (Jedrzejewski et al. 1993, Kats and Dill 1998, Herman and Valone 2000). Similarly, rodents can also evaluate information about conspecifics using released scents (Christiansen 1980). It is very difficult to assess where, when and how predator or conspecific scents are released in a natural habitat, and field studies are scarce in comparison with laboratory ones (Orrock et al. 2004, Wolff 2004, Pastro and Banks 2006, Taraborelli et al. 2008, Hughes et al. 2009). To the best of our knowledge there is no laboratory or field study that has analysed how both predator and conspecific scents may influence the patterns of seed predation and dispersal by seed-caching rodents.

We used a worldwide documented plant-disperser assemblage, the dispersal of acorns by mice (Den Ouden et al. 2005, Gómez et al. 2008) as a study model to analyse how predator and conspecific scents influence the foraging decisions of rodents. Specifically, we chose two widely distributed Mediterranean oaks (*Quercus ilex* and *Quercus pubescens*) to check the potential influence of differences in seed size and nutritive composition on rodent foraging behaviour (Perea et al. 2012). The acorns of both species are usually dispersed by the wood mouse (*Apodemus sylvaticus*) (Den Ouden et al. 2005, Muñoz and Bonal 2007, Muñoz and Bonal 2011, Perea et al. 2011b), which in turn is predated in large numbers by a specialist terrestrial carnivore, the genet (*Genetta genetta*) (Lodé et al. 1991, Hamdine et al. 1993). We hypothesize that the decisions by *A. sylvaticus* as to whether to predate or disperse an acorn, as well as how far and where to disperse it, will vary according to the presence of the scents of genets (perceived predation risk) and conspecifics (perceived pilferage risk) in the site where acorns are found. We predict that in sites with predator scents mice will show more apprehensive behaviours and modify their foraging activity by investing more time in anti-predator behaviours (e.g. vigilance) than in food searching (e.g. sniffing and acorn handling), thus reducing the rate at which acorns are predated or dispersed. In sites with conspecific scents we predict that rodents will show foraging decisions aimed at reducing acorn pilferage risk, such as avoiding the sites of higher rodent activity for acorn caching (Muñoz and Bonal 2011).

METHODS

Experimental design and data sampling

The field work was carried out in November - December of 2011 in Can Balasc field research station in the core area of Collserola Natural Park, a mature old-coppiced oak forest (ca. 170 ha) with continuous canopy cover and abundant shrub cover (see, Espelta et al. 2008 for details of the structure of oak forests in the area). During the experiment the abundance of *A. sylvaticus* could be considered high since just before and after the experiment we captured 30 and 41 different *A. sylvaticus* individuals respectively (P. Sunyer, unpublished results). We found no evidence of the presence of other rodent species, either in the video recordings or captured in the Sherman traps. The presence of genets is well documented at the study area (Llimona et al. 2007). We also found direct evidences from camera traps, video recordings and fresh excrements. Genets often accumulate faeces in latrines and the excrements are impregnated with a persistent, intense scent produced by musk glands that may play a role in intra-specific communication (Palomares 1993). We monitored one of these latrines at the study area with a camera trap. This revealed the presence of at least three different genets using the latrine (A. Garmendia pers. com.). Moreover, inside the genet faeces we have periodically located subcutaneous microchips that we use to identify our *A. sylvaticus* individuals on the trapping campaigns.

To monitor the patterns of acorn predation and dispersal by wood mice, we used acorns tagged with a 40 cm long wire attached with bright purple flagging tape at the end with an alphanumeric code written on it. This method makes it possible to easily locate dispersed seeds and does not influence seed dispersal behaviour by rodents (Forget 1990, Muñoz and Bonal 2007, Muñoz and Bonal 2011). Tagged acorns were assigned to three different scent treatments: predator scent (genet), conspecific scent (wood mouse) and control scent (water). Scent treatments were distributed over 20 plots, each including one predator treatment, one conspecific treatment and one control treatment. The 20 plots were set at a minimum distance of 25 m from each other, and the three treatments within each plot were separated by 5 m, forming an equilateral triangle and ensuring that the three scent treatments were placed in similar microhabitat conditions (i.e. under shrubs). We considered a separation of 5 m between the three scent treatments within each plot to be enough to ensure that wood mice would be able to discriminate between the different scents as previous studies with other rodent species have reported they can assess and differentiate odours at distances shorter than 75 cm (Dickman 1992, Englehart and Müller-Schwarze 1995, Russell and Banks 2007). In every treatment at each plot, we placed six tagged acorns: three of *Q. pubescens* and three of *Q. ilex*, of three size

categories (large = 7.0 ± 0.2 g, medium-sized = 3.1 ± 0.1 g and small = 1.4 ± 0.0 g) in order to distribute acorn species and size equally among experimental treatments. Thus, a total of 360 acorns were monitored by the thread-marking method. All tagged acorns were sound, as scatter-hoarding rodents usually neglect insect-infested acorns (Steele et al. 1996, Muñoz and Bonal 2008a). In each treatment the six tagged acorns were protected inside 40x40x20 cm wire cages with a mesh size of 5x5 cm to avoid acorn predation by other seed consumers (Muñoz and Bonal 2007, Muñoz and Bonal 2011).

The scents of genets for the predator treatment were obtained by mixing water with fresh genet excrements collected in the latrine of the study area in a plastic sprayer. Conspecific scent was prepared in the same way, by mixing water with fresh excrements collected from four different wood mice individuals (two males and two females) kept separately in captivity during the experiment and then released. Two handfuls of cotton were attached to the cages with plastic flanges in each scent treatment (Orrock et al. 2004). The three cages of each plot were tagged as “Genet” (G), “Rodent” (R) and “Control” (C). Once the six tagged acorns were placed in the cages, we sprayed the corresponding scent treatment onto the handfuls of cotton attached to the cages and onto the borders of the cage, but not directly onto the acorns. The water treatment served to control the potential effects of spraying (e.g. changes in humidity) on the rodents’ decisions. We checked the tagged acorns every two days and also applied the corresponding scents to each cage in all plots. The experiment lasted three weeks and finished when we detected that rodents had stopped using experimental acorns during four consecutive days. This probably happened because, once fresh acorns are dropped on the forest floor, they get dry as weeks go by (see Espelta et al. 1995), thus becoming a less profitable food source for rodents. At that stage there were on average 2.3 ± 0.5 acorns left per cage (~40%). In each monitoring session, tagged acorns were classified as: i) untouched, ii) predated *in situ* (inside the cage), iii) removed from the cage and uneaten and iv) removed from the cage and eaten. We searched intensively for all removed acorns looking for the fluorescent flag. We were able to find the majority of the removed acorns (except 5.5%, 11 out of 200). Once a removed acorn was found, we noted its numerical code, the dispersal distance (distance from the cage) the acorn status (eaten or intact) and the microhabitat in which it was located. Acorns eaten by rodents are easily identified thanks to the acorn shell remains still visible after predation and the characteristic teeth marks on partially eaten acorns. All these measures allowed us to calculate different variables in order to analyse the influence of scents on the patterns of acorn use: i) “the day of acorn use” (the day an acorn was manipulated), ii) “acorn predation *in situ*” (acorn predation in the cage), iii) “acorn removal” (acorn dispersed from the cage), iv) “dispersal distance” and v) “predation after dispersal” (whether a dispersed acorn was predated or not).

In addition to acorn monitoring in the three scent treatments, we also monitored the behaviour of mice with video cameras. We randomly selected four plots and placed 12 video cameras (one in each scent treatment) with infrared vision (SainSpeed F198 Car Dash DVR). The cameras were set up in plastic boxes (to protect them from the rain) attached to stakes that were nailed 1.5 m from the cages with the camera 0.5 m from the ground, so that it recorded the entire area inside the cage and the immediate surroundings. The cameras were set for continuous all-night recording on eight different nights. After revising all the video recordings (41,625 minutes), we had a total of 108 independent sequences (44 from the control treatment, 35 from the predator ones and 29 from the conspecific ones) with the presence of *A. sylvaticus* (see an example in the electronic supplementary material section, ESM. 1). We selected those in which mice were seen entering the cages, and performed a detailed analysis of their behavioural patterns. We established four categories of behaviour: “sniffing” (an exploratory behaviour using olfaction), “vigilance and freezing” (standing still on their back feet or remaining completely immobile), “handling” (grabbing and manipulating an acorn) and “other” (undetermined behaviours, quick movements and displacements) (Hochman and Kotler 2007). We found only three (out of 108) sequences that recorded an event of acorn consumption *in situ*, which tallied with previous evidences documenting that *A. sylvaticus* move the acorns to a preferred site before eating them (Muñoz and Bonal 2008b). Due to their extremely low number, acorns predated *in situ* were not included in the mice behaviour analysis.

Data analysis

The effects of the scent treatments on the foraging behaviour of *A. sylvaticus* in the video recordings were analysed by means of general linear mixed models (GLMM). We tested the effect of the scent treatment (genet, rodent, control) over the time spent by mice in the four behaviour categories (sniffing, vigilance and freezing, handling, other; Table 1), in 18 independent video sequences in which mice entered inside the cages, controlling for pseudo-replication by including the plot and the day of recording as random variables. In these analyses, response variables were log- or square root-transformed to meet the assumption of normality. General or Generalized linear mixed models (respectively, GLMM or GLZ) were used to test the effects of scent treatments on the patterns of acorn use: the day of acorn use, the day of acorn removal, the likelihood of acorn removal, the dispersal distance and the likelihood of predation of removed acorns (Table 2). In these analyses we included scent treatment (Genet, Rodent, Control), acorn species (*Q. ilex*, *Q. pubescens*), acorn weight and acorn removal day as fixed factors, and the plot as a random factor to control spatial variability. For the “acorn

predation” analysis we also introduced the logarithm of the dispersal distance as a fixed factor to assess any effect of dispersal distance on the decision to predate an acorn or not. For each GLMM and GLZ analysis different models were tested selecting the one with the lower AIC as the “best model”. Likewise, to assess the significance of the random factor we ran a Likelihood Ratio Test (LRT) between the best model with and without the random factor (see Lewis et al. 2011). Concerning the microhabitat where removed acorns were located, we ran a multiple contingency table analysis and no differences among treatments were found ($\chi^2 = 1.49$, $df = 2$, p -value = 0.48). Therefore, we did not include this microhabitat variable in further analyses. Finally, an ANOVA test was used to assess differences in predation rates among scent treatments and in the dispersal distance of the removed acorns non-predated by mice. All analyses were performed with R software (R Development Core Team 2008). Mean values are presented with the Standard Error (SE).

RESULTS

Video recordings

In the 108 video recordings the wood mouse was the only rodent species to forage in the experimental cages. We found significant differences in the behaviour of mice among scent treatments. Mice spent more time “sniffing” in rodent cages than in control or genet cages (Table 1a; Figure 1). Conversely, they spent more time in “vigilance and freezing” behaviours in genet cages than in the other treatments (Table 1b; Figure 1). No differences were found either for the total time devoted to “handling” or for the “other” behaviours among scent treatments (Table 1c and 1d; Figure 1).

Patterns of acorn predation and dispersal

The scent treatments had a strong effect on the day acorns were used by *A. sylvaticus* (Table 2a). Acorn use (either predation or removal) in genet treatments was significantly delayed (mean date of acorn use = 6.5 ± 0.6 days) with respect to rodent (5.9 ± 0.5 days) or control (5.6 ± 0.5 days) treatments. Particularly, acorn removal from cages with genet scents was delayed (mean date of acorn dispersal = 6.6 ± 0.6 days) with respect to control (5.6 ± 0.5 days) and rodent (5.6 ± 0.5 days) treatments (Table 2b). Regardless of scent treatments, acorn traits also affected the rates of acorn predation *in situ* and removal. Concerning predation *in situ*, *A. sylvaticus* preferred *Q. ilex* acorns (91%) over *Q. pubescens* ones and, for the two oak species, the smaller acorns ($F_{1,220} = 18.24$, $p < 0.0001$). Regarding acorn removal, mice

preferred bigger acorns, as the ones removed were significantly heavier than those left in the cages (respectively, Mean \pm ES: 4.2 \pm 0.2 g vs. 3.5 \pm 0.2 g; Table 2c).

Variable	df	Parameter	SE	P	AIC		LRT	
					Model with random factor	Model without random factor	L. Ratio	P
A. <i>Sniffing</i>					72.29	70.37	0.07	0.787
Intercept	16	6.95	0.82	0.000				
Genet	16	-0.97	0.90	0.299				
Rodent	16	2.20	0.86	0.022				
B. <i>Vigilance & freezing</i>					31.21	30.73	1.52	0.217
Intercept	16	0.65	0.20	0.005				
Genet	16	0.73	0.23	0.006				
Rodent	16	0.01	0.24	0.958				
C. <i>Handling</i>					42.69	42.62	1.93	0.165
Intercept	16	1.10	0.34	0.005				
Genet	16	0.09	0.31	0.777				
Rodent	16	-0.69	0.34	0.059				
D. <i>Others</i>					24.70	22.70	1.33E-09	1
Intercept	16	0.94	0.134	0.000				
Genet	16	0.27	0.19	0.181				
Rodent	16	-0.28	0.19	0.163				

Table 1. Results from the general linear mixed models (GLMM) assessing the effect of scent treatments (Genet, Rodent, Control) on the foraging behaviour of Wood mice (Sniffing, Vigilance and freezing, Handling, Others). Results from the Likelihood Ratio Test (LRT) assessing the significance of the random factor are also presented. See Material and Methods for a thorough description of every model.

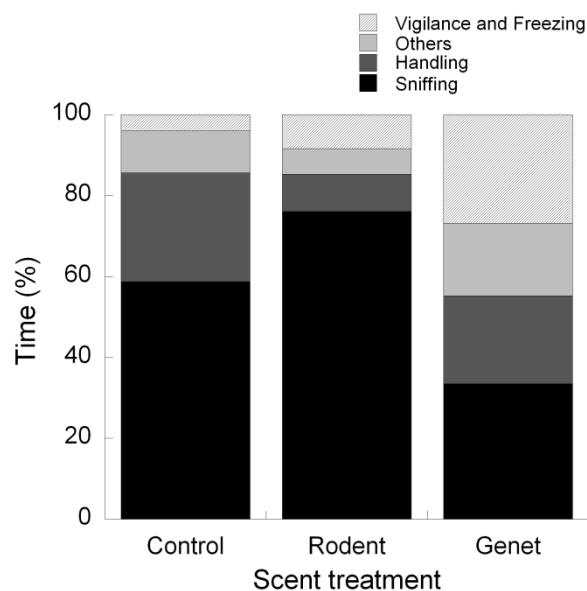


Figure 1. Time devoted by *Apodemus sylvaticus* to sniffing, handling, vigilance, freezing, and other behaviours when foraging in feeding plots with different scent treatments (control, rodent, genet).

	Variable	df	Parameter	SE	P	AIC		LRT	
						Model with random factor	Model without random factor	L. Ratio	P
A.	<i>Handling day</i>					84.67	130.99	48.32	<.0001
	Intercept	221	0.63	0.05	0.000				
	Genet	221	0.14	0.05	0.002				
	Rodent	221	0.07	0.04	0.128				
B.	<i>Removal day</i>					1.108.01	1.171.24	65.22	<.0001
	Intercept	198	1.74	0.14	0.000				
	Genet	198	0.24	0.10	0.019				
	Rodent	198	0.03	0.10	0.781				
	Q.ilex : weight	198	-0.02	0.02	0.109				
	Q.pubescens : weight	198	-0.05	0.03	0.039				
C.	<i>Removal</i>					440.70	529.90	91.20	<.0001
	Intercept	358	-0.31	0.40	0.427				
	weight	358	0.16	0.05	0.001				
D.	<i>Distance</i>					261.60	261.14	1.54	0.215
	Intercept	185	2.03	0.11	0.000				
	Genet	185	-0.10	0.08	0.217				
	Rodent	185	-0.24	0.08	0.002				
	weight	185	-0.01	0.02	0.782				
	day	185	-0.03	0.01	0.041				
	weight : day	185	0.01	0.01	0.026				
E.	<i>Predation on removed</i>					245.51	269.58	26.07	<.0001
	Intercept	185	-4.26	1.60	0.008				
	Genet	185	0.19	1.21	0.876				
	Rodent	185	-2.48	1.05	0.018				
	Q.pubescens	185	0.75	0.85	0.381				
	day	185	-0.02	0.13	0.859				
	distance	185	2.97	0.67	0.000				
	Genet : day	185	0.13	0.17	0.451				
	Rodent : day	185	0.39	0.16	0.016				
	Q.pubescens : day	185	-0.27	0.13	0.041				

Table 2. Results from the general or generalized linear mixed models assessing the effect of scent treatments (Genet, Rodent, Control), species (*Q. ilex*, *Q. pubescens*), acorn weight, dispersal distance of acorns and day of acorn removal on the patterns of acorn use: the day of acorn handling (Model A), the day of acorn removal (Model B), the likelihood of acorn removal (Model C), the dispersal distance of the removed acorns (Model D), and the likelihood of predation of removed acorns (Model E). Notice that in models A and B the day of acorn removal is not included, and that dispersal distance is only included as a fixed variable in model E. Results from the Likelihood Ratio Test (LRT) assessing the significance of the random factor are also presented. See Material and Methods for a thorough description of every model.

The rates of acorn predation *in situ* and removal did not differ among the scent treatments (see Figure 2), but the scent treatments had a strong influence on the dispersal distance of acorns (Table 2d). The acorns removed from the rodent cages were dispersed closer than those from the control cages, while those from genet cages were dispersed at intermediate distances (Figure 3). In addition, the predation likelihood of removed acorns also differed

among scent treatments (Table 2e). Acorns removed from the rodent cages were predated at lower rates (54.5 ± 6.2 %) than those removed from genet (79.3 ± 5.4 %) and control cages (66.2 ± 5.9 %) (Figure 2). We also found that acorns removed at greater distances were more often predated than those removed to closer ones (Table 2e). On the other hand, dispersal distance of non-predated acorns was similar among treatments ($F_{2,60} = 0.59$, $p = 0.56$). Ultimately, like acorn predation *in situ*, removed acorns of *Q. ilex* were preferentially predated over *Q. pubescens* ones (Table 2e).

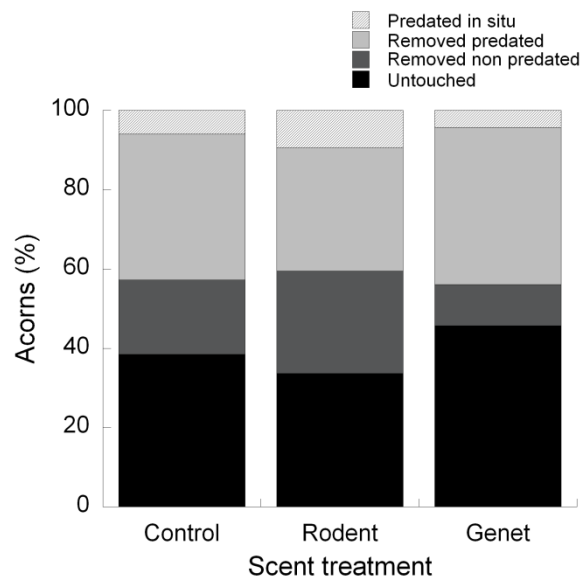


Figure 2. Final fate of the 360 acorns used in the study in relation to the scent treatments. Acorns were either predated in situ, removed and predated, removed but not predated, or untouched.

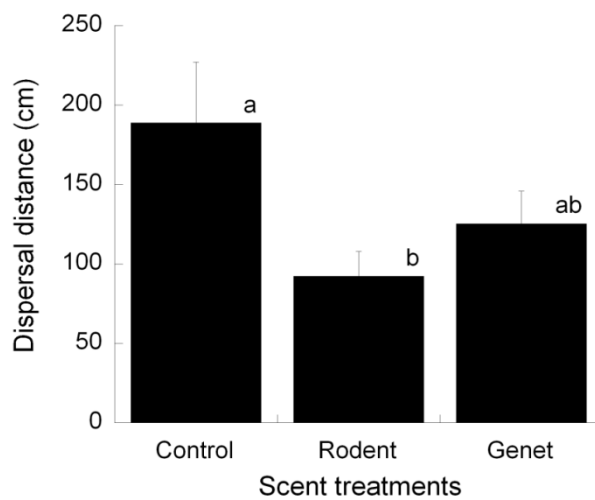


Figure 3. Mean dispersal distance (\pm s.e.) of removed acorns in relation to the scent treatments. Different letters indicate significant differences among treatments according to the Tukey test.

DISCUSSION

The present study reveals that the scents of predators and conspecifics have significant effects on the foraging behaviour of seed-dispersing rodents, and so can alter the seed dispersal patterns of plant species. Such an approach, focusing on the relevance of other factors influencing the behaviour of the dispersal agent, beyond plants' characteristics, is still less common in the literature (Crawley and Long 1995, Cousens et al. 2010, Vander Wall 2010). Hence, our study highlights the possibility that, not only plant and seed features, but also predators and conspecific competitors of seed dispersers may also play a crucial role in the ecology of seed dispersal.

The first stage in the interaction between plants and dispersers occurs when dispersers search for and find the seeds. Our results show that wood mice devoted more time to vigilance and freezing when foraging under the influence of predator scents (Figure 1), thus potentially reducing predation risk but also delaying the removal of acorns. The fact that rodents preferred to remove seeds from 'safer sites' could reduce the dispersal chances of acorns close to cues of potential predators. For acorns, such a delay in being cached could increase desiccation risk thus reducing their germination chances (see Espelta et al. 2009b for the importance of timing in the germination of acorns in these Mediterranean oaks). By contrast, when foraging under the scent of conspecifics, rodents lengthened the time devoted to sniffing (Figure 1). This increase in sniffing time may help rodents to gather information on conspecifics, but may also allow them to find and select better seeds (e.g. larger or sound), thus increasing their foraging efficiency. In any case, and conversely to what occurred in the genet cages, the behaviour of mice under the scent of conspecifics appeared to be skewed towards a more efficient assessment of the chemical environment, rather than to vigilance. The higher time devoted to vigilance in presence of predator scents suggests a trade-off between anti-predator behaviours and foraging efficiency at the stage of acorn searching (Pays et al. 2012). This may have caused the delay in acorn use in genet cages with respect to control and conspecific cages. However, we found no differential responses in acorn use between control and conspecific cages, probably because rodents may still not balance the risk of seed pilferage by conspecifics when searching for acorns (i.e. no acorns have been moved and hoarded yet). Hence, at the stage of acorn searching, only the perceived predation risk changed rodents' decisions and produced a delay in acorn use.

Once seeds have been found, the second stage in the interaction gets underway when dispersers decide what to do with the seeds encountered. During this stage, conspecific scents seem to play an important role in decision-making, probably because seed pilferage by

conspecifics will critically depend on the sites where rodents decide to move the seeds (Dally et al. 2006, Muñoz and Bonal 2011). Specifically, our results showed that conspecific scents reduced seed dispersal distances and consumption rates on dispersed seeds. This reduction may respond to the increase of acorn consumption rate with dispersal distance (regardless the scent treatment), but the interpretation may critically depend on whether consumption of dispersed seeds is due to pilferers or not (a fact that was impossible to determine). It is likely that consumption of dispersed seeds is mostly due to pilferage (Vander Wall and Jenkins 2003), and thus the reduced dispersal distance found in cages with conspecific scents would be an effective cache protection strategy (Dally et al. 2006) displayed when the rodents perceive a high risk of pilferage (i.e. in the cages with conspecific scents). Additionally, the reduction in the dispersal distance could allow animals to spend more time on seed searching as proposed by the “search time relocation hypothesis” (Jorge et al. 2012), a fact that may be especially relevant when the perceived pilferage risk of cached food is high (i.e. in the cages with conspecific scents). Finally, some sites with high conspecific activity are perceived by rodents as safer than other sites due to the microhabitat characteristics (e.g. under the tree canopy in Muñoz and Bonal 2011), so that dispersing the seeds closer to the cages with conspecific scents may be also a strategy to reduce the probability of being predated by carnivores (see however Hughes et al. 2012). To better understand the rodents’ decisions and their responses to conspecific and predator scents, it would be interesting (but difficult) to measure the rates at which dispersed seeds are pilfered or recovered by the original cacher.

Our results show that wood mice use chemosensory cues to assess the presence of predators and conspecific competitors. We observed in our video recordings that this species often gathers information on the environment by sniffing and, given its different responses to both kinds of scents, it seems that it is able to discriminate among them. Several studies have evidenced that many animals use olfaction to detect predators and conspecifics (e.g. birds, Amo et al. 2012; reptiles, Amo et al. 2004; and mammals, Norrdahl and Korpimäki 2000, Taraborelli et al. 2008). Although Orrock et al. (2004) suggested that direct cues may not be reliable for assessing predation risk compared to indirect cues (e.g. habitat structure, moonlight), we found that wood mice adjust their foraging behaviour using scents (i.e. direct cues) in field conditions. This ability to detect predator and conspecific scents may provide enormous advantages to wood mice anticipating a possible fatal encounter with a genet, and may complement the information provided by other indirect cues on predation and pilferage risks such as habitat structure (Kotler et al. 1991, Manson and Stiles 1998, Muñoz et al. 2009) or moonlight intensity (Kotler et al. 1991, Perea et al. 2011a). However, it may also convey an overestimation of

predation or pilferage risk given that predator and conspecific scents may linger after they have gone (Kats and Dill 1998).

Our results also showed that, regardless of the scent treatments, seed fate was strongly influenced by seed attributes, consistent with other studies. For example, *Q. ilex* acorns were preferred over *Q. pubescens* ones, a fact that could be explained by the higher fat content of the former (see Material and Methods section, Pons and Pausas 2007). Also, smaller acorns were preferentially predated *in situ*, whereas larger ones were selectively dispersed (Jansen et al. 2002, Jansen et al. 2004, Xiao et al. 2005, Perea et al. 2012). The importance of both seed traits and chemosensory cues in determining seed fate and dispersal patterns, suggests that studies of seed dispersal ecology would benefit from including both the plant and the disperser perspectives.

Numerous studies have approached dispersal ecology by reporting the seed dispersal patterns in different systems (Vander Wall 1990, Forget et al. 1998, Jansen et al. 2002, Beck and Vander Wall 2010). However, these should be considered as ‘average behavioural patterns’ as they do not explicitly account for the spatial and temporal variability caused by the presence of conspecifics or potential predators in the area. Indeed, we have documented for the first time a spatial variability in the dispersal patterns at short spatial scales due to the individual responses of dispersers to predator and conspecific scents. This variability of responses points out that the ecology of seed dispersal is a dynamic process both spatially and temporally. This creates the need to identify and analyse the factors that influence the seed dispersers’ decisions, to have a complete picture of seed dispersal processes by animals (Cousens et al. 2010). In particular, our results indicate the importance of chemical signals, as a new dimension of the ecology of seed dispersal by small rodents, as they might entail cascading effects on the regeneration of plants. For example, in places with high predator presence, seeds will probably be removed later by rodents, thus potentially increasing the chances of desiccation (Broncano et al. 1998), infestation by insects and fungi or predation by ungulates (e.g. wild boar in our study area, Espelta et al. 2009b), potentially reducing the seeds’ chances to become seedlings. Whether the short delay shown here is sufficient for this cascading effect remains to be determined. Conversely, our results suggest that in sites where rodents do not perceive the risk of predation they may forage more efficiently. Specifically, the detection of conspecific scents associated with a ‘safe site’ reduces the probability of dispersed seeds being predated, therefore increasing dispersal efficiency and potentially plant reproductive success. Ultimately, our results suggest that the relationships among different levels of a trophic web are quite complex. In our Mediterranean oak forest, a specialist carnivore (genet) can affect the fate of plant seeds (acorns) by altering the foraging behaviour of seed dispersers (small rodents). Further studies

will help to shed light on how these intricate processes may affect the natural regeneration of plants.

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CHAPTER 4

The interplay among acorn abundance and rodent behaviour drives the spatial pattern of seedling recruitment in mature Mediterranean oak forests

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SUMMARY

The patterns of seedling recruitment in animal-dispersed plants result from the interactions among environmental and behavioural variables. However, we know little on the contribution and combined effect of both kinds of variables. We designed a field study to assess the interplay between environment (vegetation structure, seed abundance, rodent abundance) and behaviour (seed dispersal and predation by rodents, and rooting by wild boars), and their contribution to the spatial patterns of seedling recruitment in a Mediterranean mixed-oak forest. In a spatially explicit design, we monitored intensively all environmental and behavioural variables in fixed points at a small spatial scale from autumn to spring, as well as seedling emergence and survival. Our results revealed that the spatial patterns of seedling emergence were strongly related to acorn availability on the ground, but not by a *facilitation* effect of vegetation cover. Rodents changed seed shadows generated by mother trees by dispersing most seeds from shrubby to open areas, but the spatial patterns of acorn dispersal/predation had no direct effect on recruitment. By contrast, rodents had a strong impact on recruitment as pilferers of cached seeds. Rooting by wild boars also reduced recruitment by reducing seed abundance, but also by changing rodent's behaviour towards higher consumption of acorns *in situ*. Hence, seed abundance and the foraging behaviour of scatter-hoarding rodents and wild boars are driving the spatial patterns of seedling recruitment in this mature oak forest, rather than vegetation features. The contribution of vegetation to seedling recruitment (e.g. facilitation by shrubs) may be context dependent, having a little role in closed forests, or being overridden by directed seed dispersal from shrubby to open areas. We warn about the need of using broad approaches that consider the combined action of environment and behavior to improve our knowledge on the dynamics of natural regeneration in forests.

Key words: *Apodemus sylvaticus*, *Quercus ilex*, *Quercus pubescens*, seed dispersal, seed predation, *Sus scrofa*

INTRODUCTION

Seedling recruitment in forests results from the sequential interaction among different processes, from seed production, to dispersal, predation, and finally, seedling establishment. Therefore, the whole process is not easy to approach given the great number of variables involved and the difficulties to establish relationships among them. Consequently, most studies focus on specific stages, or in some of the variables involved (see the review by Clarck et al. 1999), while few have tried to provide a "complete picture" of the whole story (but see Crawley and Long 1995, Pulido and Díaz 2005, Espelta et al. 2009a).

In addition to the inherent complexity that results from the interdependence of several sequential processes, the interaction among the behavior of seed dispersal agents (e.g. depredate or caching seeds) and environmental factors (e.g. *facilitation* effects) may also strongly influence the success of the recruitment process (Clarck et al. 1999, Crawley and Long 1995, Calviño-Cancela 2002, Gómez-Aparicio et al. 2005, Spiegel and Nathan 2012). We know, for example, that the behavior of animals such as scatter-hoarding rodents may strongly shape the patterns of natural recruitment in many plant species, acting either as seed dispersers or predators (Nathan and Muller-Landau 2000, Vander Wall 2002). From an animal-centered perspective, seed attributes, such as the species or size are known to influence the dispersal vs. predation decision (Pérez-Ramos et al. 2008, Wang and Chen 2009, Perea et al. 2012, Sunyer et al. 2014). Likewise, environmental variables such as shrub cover (Pérez-Ramos et al. 2008, Hughes et al. 1994, Perea et al. 2011a), or intra-guild competition (e.g. ungulate presence in, Focardi et al. 2000, Muñoz and Bonal 2007, Muñoz et al. 2009) are known to influence foraging decisions. From the plant perspective, it has been documented that recruitment likelihood may depend on seed abundance (see Crawley and Long 1995), microhabitat availability (e.g. *facilitation* (Gómez-Aparicio et al. 2005, Gómez-Aparicio et al. 2008, Urbietta et al. 2008), and seed/seedling consumption by granivores and herbivores (Crawley and Long 1995, Muñoz and Bonal 2007, Gómez and Hódar 2008). However, most studies focused on seed dispersal behavior have rarely tested its real contribution to seedling recruitment (but see Muñoz and Bonal 2011, Steele et al. 2011, Pérez-Ramos et al. 2013a) while those studies centered in plant recruitment have rarely provided evidences on the contribution of foraging behavior by seed predators/dispersers in this process.

To provide an integrative view, it is necessary a sequential-stage approach where the different stages, from seed production to seedling recruitment, are considered in light of the interplay among both environmental and behavioral traits (Muñoz and Bonal 2011, Wang et al. 2013). A spatially explicit design can be helpful to improve our knowledge on the relationships

between these variables, and their contribution to the patterns of seedling recruitment. Measuring a collection of environmental (e.g. seed availability, shrub cover or presence of ungulates) and behavioural (e.g. seed dispersal, seed predation, seed caching) variables in fixed points at a small spatial scale may allow to assess their spatial variation and relationships over short distances. It is known that environmental variables may vary dramatically in small spatial scales (Fortin and Dale 2005), and some studies have recently questioned if they have a fixed effect over disperser's behavior and seed fate, or their effects are strongly context dependent varying in space and time (Sunyer et al. 2014, Pérez-Ramos et al. 2013a, Wang et al. 2013, Xiao et al. 2013). This suggests that animal foraging behavior may be also highly heterogeneous at a small spatial-scale and may partly account for the heterogeneous spatial patterns in seedling establishment in combination to environmental features (Gómez-Aparicio et al. 2005, Beckage and Clarck 2003, Jurena and Archer 2003). Moreover the relevance of environmental vs. behavioral variables for seedling recruitment may be expected to be highly context dependent and vary in different ecological scenarios or according to the tree species involved. In fragmented landscapes with low vegetation cover the presence of shrubs may play a key role in facilitating seedlings establishment (e.g. providing shelter to seed dispersers in Manson and Stiles 1998, Muñoz et al. 2009; ameliorating environmental conditions in Gómez-Aparicio et al. 2005, 2008, Smit et al. 2008, 2009) while in more continuous forests, seedlings establishment may be more dependent on seed availability (Espelta et al. 2009a), or the presence of gaps (Zavala et al. 2011). Similarly, the recruitment of seedlings of co-occurring tree species may be mediated by species-specific differences in the behavior and preferences of seed predators (see for the effects of differences in seed size Espelta et al. 2009b) or dispersers (see for effects of differences in phenology Sunyer et al. 2014), and the relative tolerance of these species to environmental stresses (Espelta et al. 2005).

The recruitment of oak species in Mediterranean forests is an excellent study model to assess the role of the interactions among animal's behavior and environment on the establishment of seedlings. Oaks produce big sized seeds (acorns), which are highly nutritious and are a precious food source for many animal species such as rodents (e.g. the wood mouse, *Apodemus sylvaticus*; Muñoz and Bonal 2011, Gómez et al 2008) or ungulates (e.g. the wild boar, *Sus scrofa*; Focardi et al. 2000). Wild boars may have a strong impact on oak's recruitment, since they consume great amounts of acorns from the ground (Focardi et al. 2000), and also kill many emerged seedlings with their rooting activity (Gómez and Hódar 2008). On the other hand rodents do not only consume a lot of acorns, but also disperse them actively along the forest microhabitats (Muñoz and Bonal 2007, Muñoz and Bonal 2011, Gómez et al. 2008), and eventually cache them as food reserves, potentially aiding their germination (Vander

Wall 1990). However many of the seeds placed in buried caches end up being pilfered by other rodents, which may consume them immediately or cache them in a new location (for a review, see Vander Wall and Jenkins 2003). The main objective of this study was to assess the variability of environmental and behavioral factors involved in the interactions between seed-dispersing rodents and oaks in a mature Mediterranean mixed oak (*Q. ilex*, *Q. pubescens*) forest, in order to analyze their relevance and how they are inter-connected and linked to the patterns of seedling establishment. Specifically, we assessed the variability of the environmental variables involved in the recruitment process (acorn abundance, tree canopy and shrub cover, and rodent abundance) and the behavioral ones (seed predation/seed dispersal patterns and cache pilferage activity by rodents, and wild boar activity). Then, we tested the influence of environmental features on rodent behavior and we determined the contribution of these two sets of variables in the patterns of seedling recruitment

METHODS

Experimental design

To perform a spatially-explicit approach we delimited the study area by marking 132 fixed points with tagged wooden stakes forming a grid with a 10-meter separation among them, and georeferenced with a sub-metric GPS (Geo Explorer 6000 Series XH, Trimble). The location of the grid was selected to ensure that a half of the points (65) were placed inside an area where wild boars were excluded by means of a 2-meter high metallic fence, while the rest of points (67) were placed outside the enclosure. From November 2010 to June 2011, we monitored different environmental and behavioural variables involved in the process of natural regeneration at each of the marked points. The variables measured were:

i) *Tree and shrub cover*. If well at a first sight the shrub cover may seem continuous, it is not at all homogeneous at the fine scale of the study, as some areas are much more open than others. Hence, at each marked point we determined visually the percentages of shrub cover and tree canopy cover on a circular area with 1-meter radius from the wooden stake.

ii) *Availability of acorns on the ground*. We monitored the availability of acorns on the ground every 25 days (9 samplings) from November to June. At each sampling, we counted all the acorns on a circular area of 1 meter radius from every stake, distinguishing species membership (*Q. ilex*, *Q. pubescens*) and condition (sound or infested by insects).

iii) *Abundance of rodents*. Monitored by means of Sherman live-traps (23.5 x 8 x 9 cm; HB Sherman Traps Inc. Tallahassee, Florida USA) every 25 days (9 different campaigns) from

November to June. In each campaign, we placed 132 traps (one per stake) baited with a mixture of flour and tuna in oil, a piece of apple to avoid dehydration, and a handful of hydrophobic cotton so that the captured rodents could make a nest to keep warm until they were marked and released (see for this methodology Muñoz et al. 2009). The traps were set for four consecutive nights at sunset (i.e. 20:00 hours GMT) and were checked every morning at sunrise (i.e. 07:00 hours GMT) to minimize the captivity duration. Captured rodents were marked with a subcutaneous microchip (MUSICC, AVID Identification Systems Inc) using a specialized syringe (AVID SUDS monoject) and immediately released at the exact same point where they were caught.

iv) *Wild boar rooting activity*. Estimated visually by noting the percentage of the ground surface affected by the rooting activity every 25 days (9 different surveys) along the entire seeding season within a circle of a 1-meter radius from each stake located outside the enclosure to exclude ungulates.

v) *Predation/dispersal patterns of acorns by rodents*. The patterns of seed predation and dispersal by rodents were measured with marked acorns in 40 feeding plots distributed across the study area (20 points out of the enclosure and 20 points inside). Each feeding plot consisted of a wire cage with a mesh size of 5x5 cm in which the marked acorns were placed, ensuring that only scatter-hoarding rodents would have access to them (Sunyer et al. 2014). Acorns were marked with a 40-cm-long wire with a flagging tape (Xiao et al. 2006). We placed 320 tagged acorns along the 40 sites so that each feeding plot had eight acorns: four of *Q. pubescens*, and four of *Q. ilex*. We visited the feeding plots at 25 days intervals from the beginning to the end of the seeding season (7 samplings). At each visit we recorded the acorns predated *in situ* and tracked those dispersed outside the cage, noting the dispersal distance, microhabitat at destination, and their fate (predated or intact). All marked acorns were replaced in the feeding plots by new fresh ones at each monitoring, maintaining the same proportion of species. Thus, by the end of the study we had monitored the fate of 2240 acorns (= 320 acorns x 7 revisions). Those acorns that were dispersed but not eaten were left on the field and checked during the following samplings, until they were predated or re-dispersed to a new location (Sunyer et al. 2014).

vi) *Pilferage of acorn caches*. The patterns of cache pilferage by rodents were monitored by caching 268 acorns on 67 marked points (34 inside the enclosure and 33 outside). On each point, we artificially cached 4 ripe acorns (2 of *Q. ilex* and 2 of *Q. pubescens*) at 3 cm deep simulating the caches made by rodents (Muñoz and Bonal 2011), at a distance of 0.5 meters from the stake following the cardinal points to enable their monitoring. Acorns cached

were monitored every 25 days along the entire seeding season (9 visits) and we registered whether they were intact, pilfered, desiccated, germinated, or had produced a seedling.

vii) *Seedling emergence*. Finally, once emergence period had finished (May) we measured the emergence of oak seedlings at every marked point. We counted all the emerged oak seedlings of each species (*Q. ilex* and *Q. pubescens*) in a surface of 1-meter radius from the stake of all sampling points. In addition, we tagged all the seedlings with plastic ties and returned next year to check seedling survival. It should be stressed that this study was performed over a single year, so that the results do not account for interannual variability in climatic conditions (such as temperature and rainfall). However, previous studies have emphasized that in these oak forests early recruitment processes are of paramount importance to explain the regeneration patterns observed (see Espelta et al. 2009a)

Data analysis

To validate the consistency of the monitored variables and to consider their categorization, we initially performed a descriptive analysis of each variable noting the minimum and maximum values, the mean and standard deviation, the number of observations, the missing values, and their distribution. We also calculated the coefficient of variation (CV) for each factor as a measure of their spatial variability among the sampling points along the study area.

We used generalized linear models (GLM) with a binomial distribution and a logit link function to analyze the factors affecting rodent's foraging behavior: number of acorns manipulated, number of acorns dispersed, and number of acorns predated (over the 56 tagged acorns supplied in each feeding plot along the study), and the number of caches pilfered (over the four artificial caches placed in each sampling point). Moreover, we used GLM with a normal distribution to assess the factors affecting the acorn dispersal rates (number of acorns dispersed relative to the number of acorns manipulated, including dispersed and consumed *in situ*, for each point), and species preferences (number of manipulated *Q. ilex* acorns relative to the total number of manipulated acorns, per point). Finally, we also used GLM with a negative binomial distribution and a logit link to assess the factors affecting the emergence of oak natural seedlings (total, and for each *Quercus* species separately) at the end of the season. To assess the existence of over-dispersion in the models we used Pearson's chi-square information criteria test. In all the different GLM we used the vegetation structure (shrub cover and tree canopy cover), abundance of acorns on the ground, abundance of rodents, and wild boar rooting

activity, as fixed independent variables. For the models assessing the emergence of oak seedlings (total and for each *Quercus* species) we only considered the abundance of sound acorns since the infested ones have extremely low probabilities of germinating and producing viable seedlings (Muñoz et al. 2014). In addition to the abovementioned independent variables, in this particular model we also included the pilferage rates of caches as an explicative variable to directly test for its potential effect on seedling establishment. Moreover, for the models assessing seedling emergence of each species separately we also introduced a variable representing the relative abundance of sound acorns of each species ($Q. ilex$ acorns / $Q. pubescens$ acorns) on the ground.

The selection of significant variables for all the models was carried out by backward automatic procedure, assuming a signification level of $p < 0.05$. To build the models we used categorized values for canopy cover ($< 85\%$ and $\geq 85\%$), shrub cover ($\leq 25\%$, $25 - 85\%$ and $\geq 85\%$), availability of acorns (≤ 1 acorns, $1 - 4$ acorns and > 4 acorns), and wild boar rooting activity (0% , $0 - 10\%$ and $> 10\%$), since it allowed an easier interpretation of the results. To categorize these variables we aimed for an equitable distribution of the observations among the different categories of each variable, also considering a biological criterion to establish each category. Rodent's abundance (0 to 13) and number of caches pilfered (0 to 4) remained as numerical variables as they were key factors for the models, and we believed their categorization could reduce the accuracy when testing their effects. The use of categorized variables did not affect the results since very similar models were selected when continuous values were used.

To evaluate any spatial dependence we used a test of covariance based on the ratio of residual likelihoods to compare each GLM (complete independence of Spatial Effect) with its counterpart introducing the sampling point as a residual random factor. Since no differences were found between the models in any case we finally used the simpler model (i. e. the GLM without the random factor). The significance of the fixed variables was assessed by type III test of fixed effects, and their effect was reported from the Parameter Estimates for the continuous variables (number of rodents and pilfered acorns), and from the Estimated Odds ratio and the Estimated Least Square Means (including a test of the differences of all categories, taking into account the Tukey adjustment for multiple comparison). Data analysis was performed with SAS[®] software version 9.3 (SAS Institute Inc. 2011).

This study was conducted in the protected forest of Can Balasc, in the Collserola Natural Park, in accordance to the current Spanish legislation and with a permit of the Collserola Natural Park authorities (Num: 808). Such permit was obtained after the revision and

approval of the experimental design and capture methodology by the Natural Park biologists. We did not approach other ethics committees, since the park authorities are the ones in charge of preserving the fauna and flora of the park, and assuring the animals' welfare. Hence, the approval from an external animal ethics committee was not needed.

RESULTS

The study area presented a dense and quite continuous tree and shrub canopy cover (Mean \pm SE respectively, $73 \pm 3\%$ and $61 \pm 3\%$), with a low coefficient of spatial variation (respectively, $CV = 0.41$ and $CV = 0.49$), although both ranged from 0 to 100%. Conversely, the mean abundance of acorns on the ground (3.4 ± 0.5 acorns m^{-2}) was much more variable in space, ranging from 0 in some sites to 44.9 acorns m^{-2} , and thus presenting a high CV (1.68).

We captured 264 wood mice, *Apodemus sylvaticus*, and 2 Algerian mice, *Mus spretus*, over the nine trapping campaigns. The average number of mice captured across the study area was 3.4 ± 0.2 per trap, ranging from 0 up to 13 individuals. Although there were some points with no captures, rodents were evenly distributed at the entire study area so that spatial variability of rodent abundance was quite low ($CV = 0.76$).

At the end of acorn monitoring, rodents had manipulated (predated *in situ* or dispersed) 169 of the 2240 tagged acorns offered (4.2 ± 0.6 acorns per cage). Acorn manipulation showed a moderate variability across the study area ($CV = 0.85$), and was positively influenced by shrub cover ($F_{32} = 9.7$, $p < 0.001$), and the interaction between rodents' abundance and acorn availability ($F_{32} = 7.0$, $p = 0.003$): i.e. rodent abundance increased acorn manipulation, except in those points with very few acorns naturally available. A similar pattern was also observed for the models considering just the acorns dispersed or predated (results not shown).

At the end of the experiment, 86.4% of the acorns manipulated by rodents had been dispersed from the cages ($6.5 \pm 0.9\%$). Seed dispersal rates (number of dispersed seeds respect those manipulated) ranged from 0 to 100% but showed very low variability along the study area ($CV = 0.30$). Rodent abundance had a positive effect on the dispersal rates, especially in places with lower tree canopy cover ($F_{18} = 5.2$, $p = 0.035$) and with higher abundance of acorns ($F_{18} = 5.6$, $p = 0.013$). On the other hand, rooting activity by wild boar strongly reduced the dispersal rates of acorns by rodents, especially in those places with denser tree canopies ($F_{18} = 4.0$, $p = 0.036$). Moreover, the interaction among rodent's abundance and wild boar rooting ($F_{18} = 6.1$, $p = 0.009$) revealed that rodent's positive effect on dispersal rates shifted to a negative effect in those places rooted by wild boars.

Interestingly rodent's dispersal activity changed the spatial patterns of seed shadow concerning shrub cover (Figure 1). Rodents biased seed transfer towards open places, as most acorns dispersed (95.9%) came from site under a shrub and, 44.4% of them (N = 52) were dispersed to open places. By contrast only 4.1% (N = 5) of the seeds dispersed by rodents were removed from open places, and only 2 of them were transferred to a site under shrub cover. Additionally, rodents did not show any significant differences in their preference for each species, showing similar patterns across the study area (CV = 0.56). However, the GLM revealed a positive effect of acorn abundance on the preferential selection of *Q. ilex* over *Q. pubescens* acorns mediated by shrub cover ($F_{17} = 3.8$, $p = 0.021$). Most dispersed acorns (93.9%) were finally consumed, and only 6.1% of dispersed acorns escaped predation.

Finally, we found a strong and widespread pilferage activity, as $46.3 \pm 3.6\%$ of the artificial caches placed were pilfered by rodents, (CV = 0.77). Pilferage rates were directly related to rodent abundance ($F_{65} = 5.1$, $p = 0.027$; $\beta = 0.14 \pm 0.06$), but not influenced by shrubs, tree canopy cover or rooting by wild boars

Seedling emergence (1.5 ± 0.4 seedlings m^{-2}) presented the highest spatial variability across the study area (CV = 3.1) among all measured variables, ranging from 0 to 45 emerged seedlings m^{-2} . At the end of the season the total number of emerged seedlings of each species was similar (273 of *Q. ilex* and 268 *Q. pubescens*). Overall seedling emergence was positively affected by the number of acorns available on the ground ($F_{57} = 10.8$, $p < 0.001$) (Figure 2a), and negatively affected by the rooting activity of wild boar ($F_{57} = 3.6$, $p = 0.035$) (Figure 2b). More interestingly, the pilferage activity by rodents had a strong effect on the number of seedlings emerged ($F_{57} = 27.6$, $p < 0.001$; $\beta = -0.72 \pm 0.14$) (Figure 2c). By contrast, other environmental variables like shrub cover (Figure 2d), or other behavioural variables like acorn dispersal or predation, did not influence seedling emergence. These patterns also held true when considering the seedlings of each species separately, also showing strong negative effect of pilferage activity over natural seedling emergence of each species (*Q. ilex*: $F_{51} = 9.2$, $p = 0.004$, $\beta = -0.49 \pm 0.16$; *Q. pubescens*: $F_{53} = 18.6$, $p < 0.001$, $\beta = -0.98 \pm 0.23$). Nevertheless, seedling survival after 1 year was higher ($t_{100} = 2.49$, $p = 0.014$) for *Q. ilex* (37.36 %) than for *Q. pubescens* (24.63%).

DISCUSSION

The main contribution of this study is revealing that seedling recruitment in Mediterranean mixed oak forests may show a very high spatial variability, not just mediated by a facilitation or nursing effect of shrub or tree location as often suggested (see examples in

Marañón et al. 2004), but mostly driven, in these more continuous forests, by the spatial variability in the seed shadow and the behavior of seed predators and dispersers (i.e. cache pilferage by scatter-hoarding rodents and the effects of wild boar activity). Moreover, we reported, apparently for the first time, the effect of an interesting animal-to-animal interaction influencing seed survival and recruitment likelihood: i.e. wild boar's presence modified rodent's seed dispersal/predation behavior, as they shifted from seed dispersers to the consumption of acorns *in situ* in those places rooted by boars. The importance of animal-to-animal interactions in the behavior of scatter hoarding rodents is increasingly receiving more interest (e.g. Muñoz and Bonal 2007, Puerta-Piñero et al. 2010) and providing evidences of relevant consequences for seedling recruitment of intra-guild competition (Bonal and Muñoz 2007, Peguero and Espelta 2013), or the consequences of fear of seed disperses to predators (Sunyer et al. 2013).

Seedling emergence in our study area was not related to the distribution of tree or shrub cover (Figure 2d), differing from the results of other studies in Mediterranean-type forests that have stressed a 'nurse effect' of shrubs on recruitment by means of different effects: i) the enhanced handling and selection of seeds by seed-dispersing rodents (Pérez-Ramos et al. 2008, Muñoz et al. 2009, Perea et al. 2011a), ii) suitable abiotic conditions for seed germination and seedling emergence (Gómez-Aparicio et al. 2005, 2008, Smit et al. 2008, 2009), and iii) protection of seedlings from ungulates (Gómez and Hódar 2008, Perea and Gil 2014). However, it should be stressed that these results were often derived from studies conducted in areas where vegetation cover is scarce and often distributed in a patchy pattern. In that scenario, trees and shrubs may certainly play a major role in providing shelter to seed dispersing rodents (Muñoz et al. 2009, Perea et al. 2011a), or facilitating seedling emergence and survival by reducing environmental constraints (e.g. radiation and water stress in (Gómez-Aparicio et al. 2005, Smit et al. 2008, 2009, Marañón et al. 2004). Conversely, the more dense and homogenous tree canopy cover in our study area may provide a general shelter to seedlings and thus make recruitment patterns to be more influenced by seed abundance and less dependent on the availability of shrubs as suitable microsites (see for similar results Crawley and Long 1995, Rey and Alcántara 2000, Arrieta and Suárez 2005, Espelta et al. 2009a). Indeed, our results showed that seedlings' emergence was strongly and positively related to seed abundance on the ground (Figure 2a), while scatter-hoarding rodents changed the seed shadows from shrubby towards open sites (Figure 1). This suggests that preferred site for seed-dispersal by rodents (i.e. under shrubs or to forest gaps) is not a fixed behavior but may be highly context dependent. Other studies have also documented a directed seed-dispersal by rodents to open sites (Muñoz and Bonal 2011, Perea et al. 2011b), that may be explained by the lower pilferage rates in these uncovered sites due to the higher predation risk in absence of shelter. Moreover, the behavior of

rodents observed in our study area may be extremely interesting for oak recruitment, considering that previous studies in these forests have shown that seedling establishment and growth may be ultimately constrained by the excessive shadow and competence provided by the tree layer and thus it benefits from the germination of (rodent-dispersed) acorns in gaps receiving mid radiation levels (Espelta et al. 1995, Retana et al. 1999, Zavala et al. 2011).

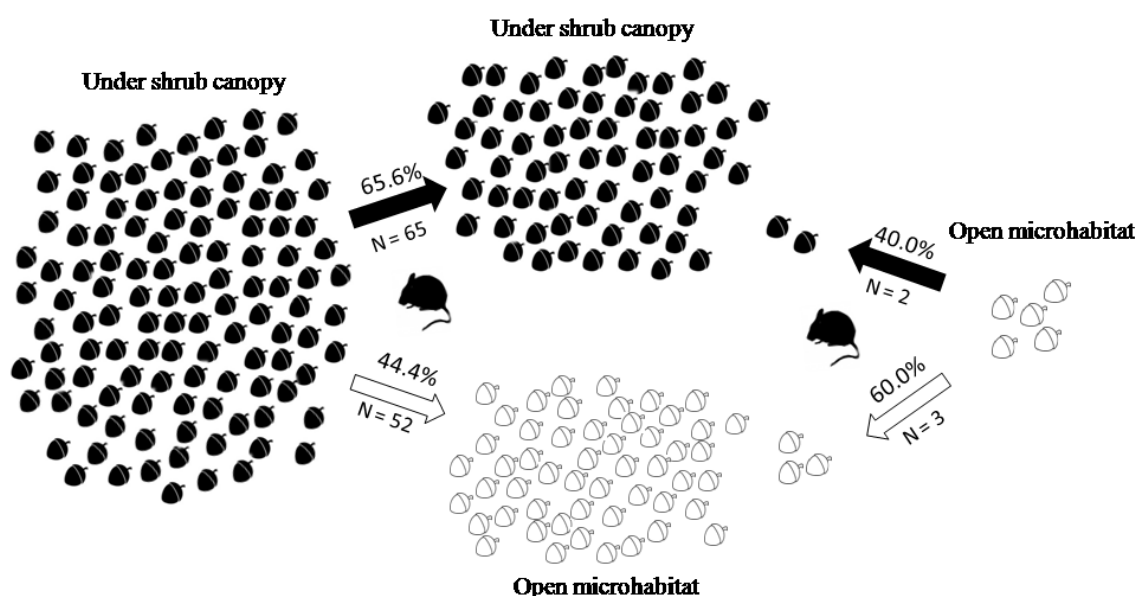


Figure 1. Graphical representation of how rodents modified the seed shadows generated by mother trees. Dark acorns represent seeds under shrub cover, and white acorns seeds on open sites.

The lack of a key effect of environmental constraints in the early seedling recruitment stages in our study area, as suggested by the absence of nursing effects, probably turned seed availability, mediated by rodent behavior (i.e. pilferage and acorn predation), to be the most relevant drivers in the process of seedling establishment (see also Espelta et al. 2009a for the effects of acorn crop size). Some studies have documented that pilferage may increase with vegetation cover, as rodents are more abundant and active in these sites (Muñoz and Bonal 2011, Steele et al. 2014), a pattern supported by the strong correlation between pilferage rates and rodent abundance found in our study area. However, one important finding of our study is that the activity of rodents as pilferers of cached seeds may ultimately influence the recruitment patterns of oaks (Figure 2c). Rodents' pilferage activity has been traditionally approached from a behavioral perspective (Vander Wall and Jenkins 2003, Dally et al. 2006, Huang et al. 2011, Steele et al. 2014). So far, pilferage has been understood as the “theft of cached food to another animal”, but to our knowledge, its impact on plant's reproduction has been less often considered

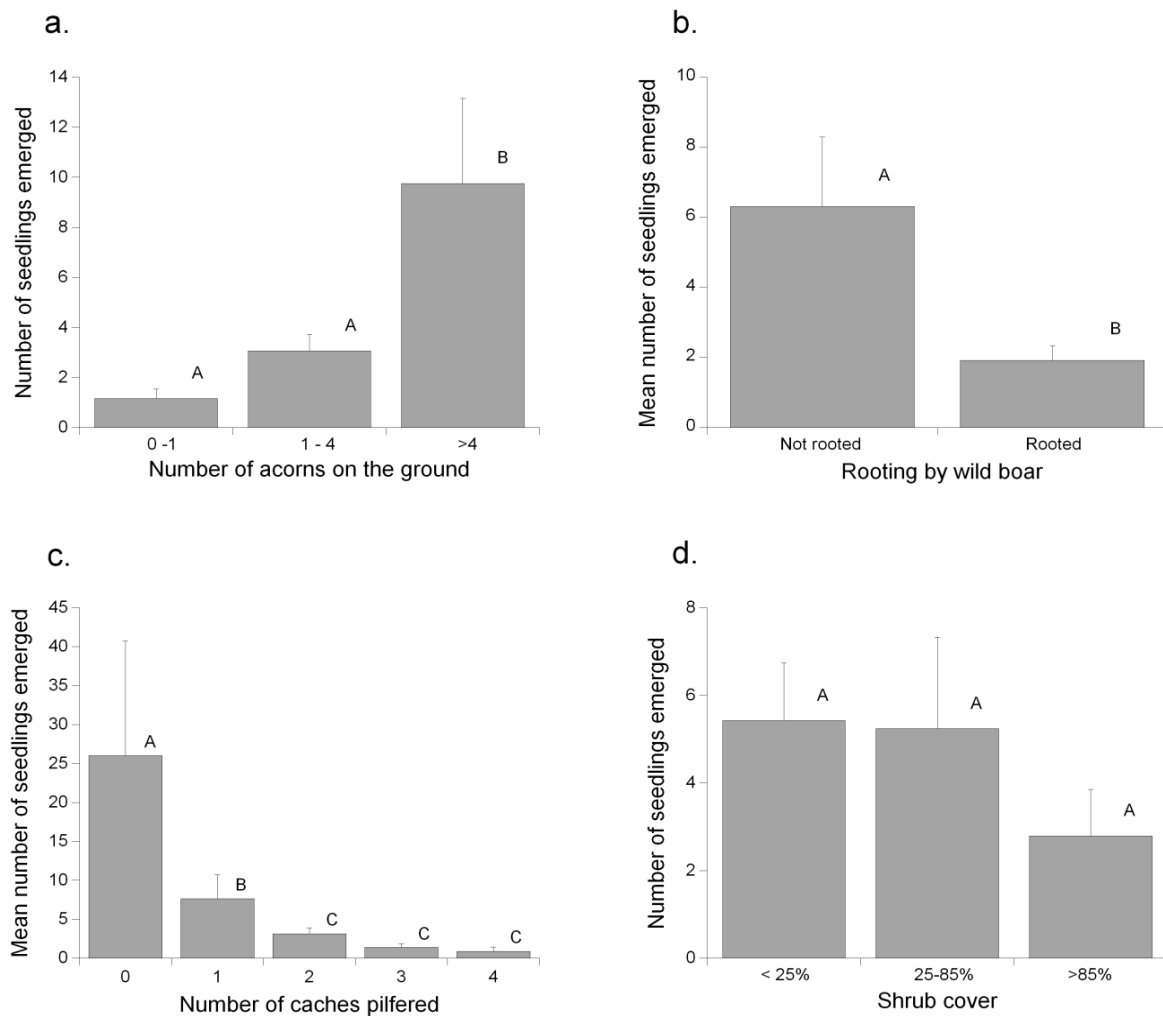


Figure 2. Effects on oak's recruitment of the number of acorns in the ground (a), wild boar rooting activity (b), cache pilferage by rodents (c), and shrub cover (d). Different letters represent statistical differences according to the Fisher LSD test. Results represented are mean values \pm standard errors.

(but see Steele et al. 2011, Smit et al. 2009). Our study provides direct evidences that pilferage may certainly have this broader dimension, as we found a negative relation between pilferage activity and recruitment: i.e. those places where rodents stole more caches had lower number of emerged seedlings. We cannot ensure whether pilfered caches were finally consumed by the rodent, or re-cached in another location, which would have no effects on the reproductive success of the plant but in its spatial distribution. Anyway, these results reinforce the hypothesis that in our forest seed availability is the most limiting factor for recruitment. In fact, seed abundance may also play an important role for seedling emergence in relation to rodent abundance, since great seed crops have been found to satiate rodents, increasing the recruitment chances for the plant (Xiao et al. 2013). Nevertheless, in our study area we did not find a direct

effect of rodent abundance on seedling emergence, probably due to the small spatial scale considered (i.e. the home range of a wood mouse individual may include several sampling points where rodent abundance and seedling emergence were measured).

In addition to seed pilferage, seedling establishment suffered a direct and indirect negative impact from the foraging activity of wild boar (Figure 2b) an abundant species in our study area (Cahill et al. 2003). Wild boars are known to directly reduce oak recruitment chance by consuming great amounts of acorns (Focardi et al. 2000), and killing the emerged seedlings when rooting (Gómez and Hódar 2008). Surprisingly, we also found an indirect negative effect of the presence of wild boar as it switched the foraging behavior of rodents, decreasing dispersal and increasing the *in situ* consumption of acorns (see also Muñoz and Bonal 2007). Certainly, in terms of optimal foraging theory, this change in behavior is reasonable in order to reduce the probability of intra-guild competition by wild boars (e.g. acorn predation and destruction of caches). Rodent's response to competition by modifying their behaviour may have important consequences for the fate of the seeds they use (i.e. consume vs. disperse), as described for fear-induced behavioural responses (e.g. Sunyer et al. 2013). These results provide new evidence of the importance of animal-to-animal interactions on the behaviour of rodents and the consequences of these interactions for the patterns of seed dispersal vs. seed consumption. Moreover, this shift in the outcome of the rodent-seed interaction represents a good example of how ecological interactions in nature may be non-monotonous, which has been found to contribute in maintaining stable and complex ecological networks (Yan and Zhang 2014).

Concerning the two oak species, the effects of environmental and behavioral variables on the recruitment of *Q. ilex* and *Q. pubescens* seedlings were very similar, except for a slightly higher preference of rodents for the acorns of *Q. ilex*, mediated by the largest acorn crops of this species, and a higher survival of the established seedlings of this oak. These results are in line with previous studies that have shown a key role of the largest acorn crop sizes produced by *Q. ilex* both for a preferential manipulation of their seeds by rodents (Sunyer et al. 2014), and for the more abundant seedling recruitment of that species in comparison to *Q. pubescens* (Espelta et al. 2008, Espelta et al. 2009a). The benefits of a largest seed availability of *Q. ilex* for seedling recruitment is complemented by the higher survival rates of this species, as shown by our results, in the current environmental conditions of this mixed oak forest types (Bran et al. 1990), while *Q. pubescens* seedlings would be favored under shadier conditions of more mature forest structures (Espelta et al. 2005).

In Mediterranean-type communities, the spatial pattern of seedling recruitment of late-successional species, such as oaks, has been traditionally assumed to depend on the facilitation

or nursing effect of the tree and shrub layers (see among others Lookingbill and Zavala 2000, Zavala et al. 2000, Zavala et al. 2011, Pérez-Ramos et al. 2013b). Yet, we have shown that in more mature forests, this protective effect may be overridden by the interplay among seed availability, rodents' behaviour and wild boar rooting. In sum, our results suggest that the relevance of facilitation for seedling recruitment and the role that rodent's activity may play as seed dispersers/predators can be highly context dependent on forest structure, varying from a great importance of facilitation in low density savannah-like landscapes to a minor role in dense forests where rodents may even contribute to the dispersal of seeds to forests gaps. Considering how the interactions among behavioral and environmental variables that we report here may affect seedling establishment, we suggest that further studies dealing with forest dynamics should incorporate this broader view to better grasp the complexity of the processes involved in forest regeneration, avoiding studies focused separately in environmental or behavioral traits. Furthermore, it would be very interesting to assess whether the interactions described here are consistent in time and may ultimately contribute to determine the forest structure.

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GENERAL DISCUSSION

How small rodents may influence plant's recruitment and forest regeneration is one of the major concerns of seed dispersal ecology. Many studies have assessed the effects of several factors on the foraging preferences by rodents, and how these may determine the final fate for seeds, thus potentially affecting plants' reproductive success (e.g. Vander Wall 2001, Pulido and Díaz 2005, Muñoz and Bonal 2008, Pérez-Ramos et al. 2008, Perea et al. 2011, Pérez-Ramos et al 2013, Wang et al. 2013). Generally, the “take home message” of these studies is that certain rodent species is a disperser or a predator of certain plant species, providing information on a particular stage or some aspect of the interaction (e.g. seed choice, seed movement, seed pilferage, seed germination and plant recruitment; Daly et al. 1992, Xiao et al. 2005, Takahashi et al. 2007, Wang and Chen 2008, Chang et al. 2012). However, the questions on how and why rodents change their foraging behaviour in space and time, and what effects this may have for the plant, have been seldom considered. The inclusion of space and time as variables leads to consider that the role of certain rodent species as disperser or predator of certain plant species can be more context-dependent than previously believed (see Zwolak and Crone 2012). A main contribution of the present thesis deals with this issue, highlighting the need of contextualizing the decision-making process by rodents to have a more realistic picture of the plant-animal interaction.

Rodent's foraging behaviour: learn and adapt vs. inherited patterns

We have documented that the interactions between scatter-hoarding rodents and plants may change in space and time, depending on the influence of a great variety of temporally- and spatially-heterogeneous interacting factors. These spatial and temporal changes are mostly due to the behavioural flexibility of rodents, which allow them to adapt and respond to the environmental circumstances of a given site in a given time (e.g. food availability in Khames and Aulagnier 2007, Unnsteinsdottir and Hersteinsson 2011). We have shown that seasonal variations in acorn availability on the ground have an important influence on the population dynamics of wood mice (chapter 1). In this case, behavioural flexibility seems not to be enough to cope with the lack of acorns during summer, when rodent survival decrease and the population experiences a strong decline. During the seeding season, temporal variations in mouse abundance may lead to changes in their seed foraging decisions, and thus seed's fate, as

the conspecific presence perceived by rodents increases their seed dispersal vs. seed predation ratio (chapter 3). This can also have a spatial dimension when the distribution of rodents is aggregated, so that there might be areas with higher densities than others (e.g. under shrubs Herrera 1995, Muñoz and Bonal 2007, Pons and Pausas 2007, Muñoz et al. 2009). Altogether, our results suggest that rodent's foraging decisions and seed dispersal patterns may change in space and time according to rodent population densities, which in turn may depend on the phenology of seed fall by the plant (chapter 1). This highlights the close interplay and mutual dependence between wood mice and oaks in Mediterranean oak forests. More interestingly, in the chapter 2 we evidenced that rodents are able to adapt their acorn choices to the most abundant acorn species available on the ground, thus changing their preferences along the same seeding season as a consequence of the phenological mismatch in acorn fall between *Quercus pubescens* and *Q. ilex*. Rodents adapting their acorn preference to the most abundant acorn species may have an advantage over those showing a fixed preference, as the relative availability of each acorn species may differ strongly within and between years (Espelta et al. 2008, 2009, Fernández-Martínez et al. 2012). Although some studies have documented that rodents have a fixed seed species preference (Gómez 2004, Pons and Pausas 2007), they did not control for the relative abundance of each seed species, so that actual preferences could be better explained by the relative availability of seeds than by their chemical or physical characteristics. The temporal changes in acorn species preference by rodents along the seeding season, reported in chapter 2 have not a spatial dimension at a fine scale (chapter 4), so that these temporal changes are consistent across the study area.

The interaction of wood mouse with other animals also had important effects on the patterns of seed predation and dispersal. In chapter 3, we found that wood mice are able to detect and respond to chemicals released by genets (*Genetta genetta*), their most prominent specialized predator (up to a 79% of the small mammals in its diet; Torre et al. 2003). Mice initially avoided foraging in areas with chemical cues of genets, also showing a more vigilant and less efficient foraging behaviour (chapter 3). In this case, an inherited fixed behaviour display is more advantageous than a learned-flexible behaviour, given that the outcome of an interaction with a genet (the death of the rodent) does not allow the possibility to learn. This instant recognition of a predator scent as dangerous allows managing a rapid behavioural response, such as delaying acorn dispersal, to reduce predation risk (chapter 3). Moreover, in chapter 4 we found that wild boar (*Sus scrofa*) rooting increased the consumption of seeds *in situ* by wood mice, and decreased seed dispersal rate. This behavioural bias is consistent with an optimal foraging strategy aimed at maximizing the energy gain relative to the costs of foraging, as acorns dispersed and cached by rodents can be pilfered by wild boars (Focardi et al. 2000,

Suselbeek et al. 2014). Despite their effect on rodent foraging behaviour, wild boars have not a significant influence on the wood mouse population dynamics at the study area (chapter 1).

Mediterranean habitats present very heterogeneous and unpredictable conditions, with marked inter- and intra-annual variability in environmental factors, such as climate and food abundance (Blondel and Aronson 1999). For a wood mouse, which have very few chances of living more than one year (chapter 1), a flexible behaviour may be evolutionary advantageous over a fixed one, since its close relevant environment (e.g. acorn abundance, weather, predation risk, acorn competition) may strongly change not only among different rodent generations, but also within the life span of a single rodent. Although most factors that influenced wood mice decisions varied in space and time, their preference for certain acorn attributes (i.e. large and sound acorns; chapters 2 and 3) did not change in time and space, suggesting that some variables may have a rather fixed effect on rodent choices. In general, an inherited fixed behavioural response is more advantageous for factors that have an unchanging influence and that impose important pressures to animals. In contrast, other circumstances with less dramatic consequences, like the proportion of acorn species available, or cache pilferage risk, allow a major flexibility in rodent's behaviour to learn and adapt their foraging decisions (see Muñoz and Bonal 2008). In fact, most spatial and temporal variability of wood mouse behaviour documented in this thesis probably results from a rapid "learn-and-adapt" process. Bearing this in mind, it would be a great step forward to establish which behavioural displays are inherited by phylogeny (e.g. recognizing scents of a specialist predator like the genet) and which are developed during the ontogeny (e.g. adapting to environmental variability). Inherited and fixed patterns are expected to exert stronger evolutionary pressures on plants' traits than flexible patterns that change in space and time. Thus, assessing whether learned behaviours (variable) or those inherited (fixed) are more relevant for the interaction between scatter-hoarding rodents and plants may shed light in the evolution of rodent-plant interactions and life history traits of plants dispersed by rodents.

Scatter-hoarding rodents: friends or enemies of plants? a context-dependent question

Oaks and wood mice in Mediterranean forests may have co-evolved, developing many strategies to benefit one from another. However, whether this interaction can be considered as mutualism or not depends ultimately on the net effect of rodents on oak's dispersal and recruitment (Muñoz and Bonal 2011, Zwolak and Crone 2012). Wood mouse dependence on oaks is straightforward, as acorns represent the main and most abundant food resource during

the acorn fall season (reviewed by Torre et al. 2002), to the point that their population dynamics and seed preferences match the seeding phenology of oaks (chapters 1 and 2). Conversely, determining to what extent oaks depend on rodents is a more complicated question. Theoretically, oaks have developed strategies to "manipulate" seed-dispersing rodents in their favour by offering appealing seeds (e.g. large, nutritious), and also by influencing their populations and behaviour with important fluctuations in their seed crops (Vander Wall 2002, Zhang et al. 2008, Vander Wall 2010). However, this 'manipulation' suggested under a general life-history evolution framework does not necessary imply a successful outcome for the plant in a particular ecological scenario. The key issue for plants is whether some dispersed seeds will never be recovered and will have a higher recruitment success than not dispersed seeds (Vander Wall 1990, Steele et al. 2011). Many variables are involved in this process, so that the explicit connection between the patterns of plant recruitment and the foraging behaviour of seed-dispersing rodents has hardly been studied (Muñoz and Bonal 2011, Steele et al. 2011, Pérez-Ramos et al. 2013). In the spatially explicit design of chapter 4, we analysed the relationship between the patterns of oak's recruitment and wood mouse foraging behaviour at three different stages (seed predation, seed dispersal and cache pilferage). We found that, although wood mice dispersed many acorns and modified the seed shadows generated by mother trees, there was no direct connection or pattern between seed predation or dispersal and seedling recruitment at a small spatial scale. By contrast, we found a clear negative effect of rodents on seedling establishment as seed pilferers: the areas with higher pilferage rates showed lower seedling densities (chapter 4). Hence, even though it is clear that oaks are strongly affected by rodent's activity, it is difficult to establish whether wood mice foraging behaviour has either a positive or a negative effect on the regeneration of oaks (Muñoz and Bonal 2011), especially considering the flexible behavioural patterns displayed by rodents that change in space and time.

Indeed, Zwolak and Crone (2012) reviewed several studies assessing granivore-plant interactions and found that their net outcome ranged from antagonisms to mutualisms depending on the ecological context of the study, and even among particular conditions within a same study. Wood mice can be considered "friends" or "enemies" of oaks depending on the ecological context of, for example, rodent and acorn abundance, genet and wild boar presence and acorn rain phenologies, and on the temporal scale considered. In this context, it is important to highlight the difference in temporal scales between oak and scatter-hoarding rodents for estimating fitness performance and reproductive efficiency of individuals. Oaks may live for centuries, while mice have very few chances of living more than one year. If acorn production is low in certain year, it is relatively easy to measure the consequences for reproduction and fitness of rodents (chapter 1). However, seeds produced by a single oak tree along its life are predated

and dispersed by hundreds of wood mouse generations. This temporal asymmetry sets methodological difficulties for measuring the actual effects of rodents on oak fitness under an evolutionary framework (e.g. to determine whether seedlings from dispersed seeds become adult trees). Nevertheless, the chances that seeds dispersed by mice survive and successfully recruit are probably high along the whole oak's life span, in support of the general framework of co-evolution between scatter-hoarding rodents and the dispersed plants. Under this perspective, wood mice are probably more friends than enemies of oaks, or at least more friends than other seed predators that do not scatter-hoard seeds.

Bearing in mind the temporal asymmetry between oaks and rodents, the spatial and temporal variability of rodent's foraging behaviour may have an important relevance for oak life-history evolution. Fixed behaviours in time and space (such as a constant preference for dispersing a given seed phenotype), may impose stronger selective pressures to a plant, given the persistence of the behavioural pattern over hundreds of seed-dispersing rodent generations. For instance, a fixed preference for dispersing larger seeds (chapters 2 and 3), could drive plant's evolutionary history to increase seed size (Jansen et al. 2002, Xiao et al. 2005, Muñoz et al. 2012). In contrast, the behavioural flexibility may reduce the strength of selective pressures and this may favour the intraspecific variability of seed phenotypes (Muñoz et al 2012), or the coexistence of different plant species. For example, in chapter 2 we evidenced that wood mice changed their acorn species preference to the most abundant one (*Q. pubescens* at the beginning of autumn, *Q. ilex* at spring), thus allowing a window of chance for dispersal of each oak species during the same seeding season. Hence, the dispersal chances of an oak species do not depend entirely on the total acorn crop, but also on its acorn drop timing, so that not only masting (e.g. Vander Wall 2002, Shimada and Saitoh 2006) but also the acorn rain phenology may be relevant traits in life-history evolution of rodent-oak interactions.

Wood mouse-oak interaction in Mediterranean forests

We have emphasized how the relationship between scatter-hoarding rodents and seeds might vary according to changing environmental factors in space and time. In our mixed-oak forest, the spatial patterns of oak's early recruitment were related to acorn abundance on the ground at small spatial scale (chapter 4). In chapters 2 and 3, we documented that wood mice act mainly as disperser, because they prefer moving instead of consuming *in situ* the acorns. In particular, most acorns were moved from shrubs to open sites, what could have beneficial effects for seedling establishment in our dense-canopy forest. However, most dispersed acorns were finally consumed, either by the same rodent or by conspecific pilferers, thus potentially

reducing the acorns available for recruitment (chapter 4). In fact, in those sites with higher pilfering activity, the number of oak seedlings was lower.

Wild boars also had an important role in the interactions between wood mice and oaks by increasing the rate of seeds predated *in situ* vs. seeds dispersed by wood mice (chapter 4). This indirect negative effect of wild boars on oaks is added to their direct effects as prominent seed and seedling predators (Focardi et al. 2000, Gómez and Hódar 2008, Suselbeek et al. 2014). Additionally, we found that a typical Mediterranean carnivore, the genet, affected the wood mice-oak interactions by delaying the dispersal of acorns (chapter 3), which would be more susceptible to desiccation or consumption by other animals (e.g. wild boars). The indirect effects of genets and wild boars on oaks evidence the complexity of ecological interactions in Mediterranean forests. This is especially relevant considering that wild boar densities have dramatically increased in Mediterranean forests over the past years (reviewed by Massei et al. 2011) and the suitability of these forests for genet environmental requirements (Torre et al. 2003).

It is worth mentioning that Mediterranean oak forests are very variable regarding habitat structure, and thus the habitat characteristics where the interaction between rodents and plants take place also deserve special attention. For example, in open habitats such as savannah-like oak forests, that are often dryer environments, shrubs have a vital role for rodent dynamics and oak's recruitment (e.g. Pulido and Díaz 2005, Smit et al 2008, Muñoz et al. 2009, Perea et al. 2011). Moreover, in these habitats, the spatial patterns of seed predation and dispersal by rodents and the patterns of seedling recruitment are highly conditioned by the spatial distribution of scattered oaks (Muñoz and Bonal 2011). Also, the impacts of wild boars on rodent populations are more dramatic in open habitats (Muñoz et al. 2009) than in close forests. However in our close forest, the abundant shrubs were not so crucial for rodent demographic dynamics (chapter 1), or for the spatial patterns of oak's recruitment (chapter 4). Thus, given the great diversity of Mediterranean oak forest types according to the vegetation structure, and considering the complex relations among the different organisms of the trophic web, the interaction between seed-dispersing rodents and oaks may strongly differ depending on the place or the moment where it takes place.

Further perspectives

We have provided evidence that the interactions between rodents and plants may change at very small spatial and temporal scales according to factors of different nature. In order to assess how rodent's behaviour affects seed fate and recruitment, it is necessary a methodological

approach that considers explicitly the context-dependence of the interaction. We suggest that further research on seed dispersal by rodents should always bear in mind that the temporal and spatial scenario may change, having strong consequences for rodent's behaviour. In the case of fixed behavioural displays like preference for larger seeds, this does not represent an important problem, since studies performed in different moments or sites are expected to report the same patterns (Figure 1a). Conversely, for flexible behaviours like seed species preference, it is essential considering the site and moment when a study is conducted, since the results may change in time and space (Figure 1b). For example, the same study conducted in t_1 and t_2 will provide very different conclusions (preference for *Quercus pubescens* and preference for *Q. ilex*), given the temporal variation in species preference (chapter 2).

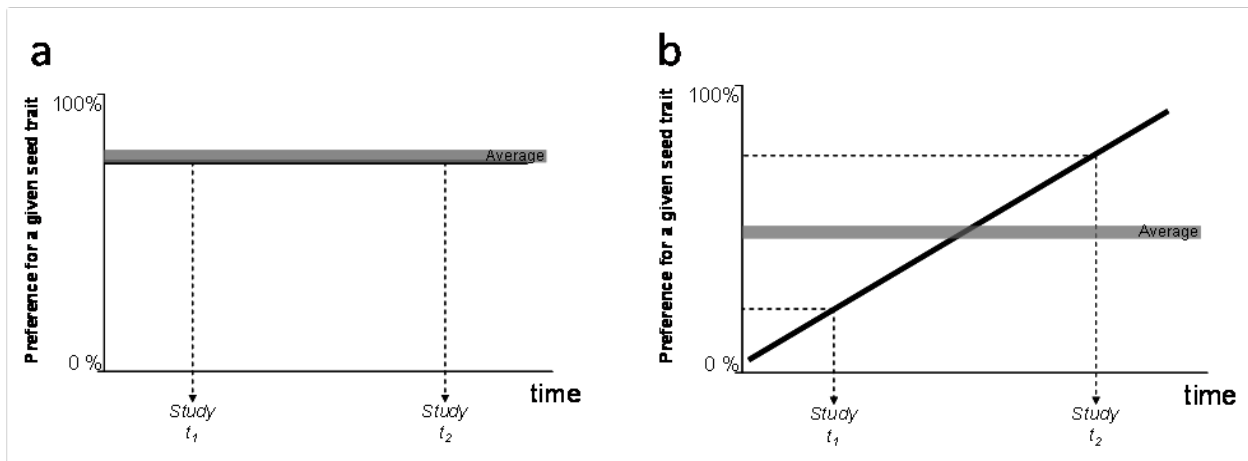


Figure 1. Theoretical changes in rodent preferences for a given seed trait along the seeding season (black line). In the graph on the left (a) rodents show a strong and constant preference for a particular seed trait. Studies carried out at any time of the seeding season will provide similar and accurate conclusions. In the graph on the right (b) rodent's preferences change with time, so that a study conducted at the beginning of the season (study t_1), will conclude that rodents show a low preference for the seed trait, while one study conducted by the end of the season (study t_2), will claim that rodents show a high preference for that trait.

We have also shown that some trophic relationships (i.e. the presence of rodent predators) may influence the interaction between rodents and plants. Hence, we suggest that further studies would benefit from considering the potential interactions between rodents and their predators and competitors to better explain some aspects of the rodent-plant interaction. Incorporating such interactions could help explain a significant proportion of the unexplained variance of rodent foraging patterns that is often viewed as random noise.

In last place, the results of this thesis encourage further studies to explore how global change could impose changes in this animal-plant interaction, since rising temperatures and lower rain fall in Mediterranean habitats could affect the phenologies and crops of acorns, and

thus the rodent population cycles. Even more, an alteration of oak's flowering and seeding phenologies could result in a potential mismatch between plant phenology and the dynamics and activity of its disperser, with important consequences for the seeds.

Summarizing, this thesis documents the spatial and temporal variability in the behavioural patterns of a seed-disperser, and highlights the outstanding importance of the context for animal-plant interactions. Considering the different sources of variability described here, we suggest extreme caution to derive general conclusions of ecological processes from punctual and specific studies that do not consider the huge array of factors and interactions involved. In this sense, a main contribution of this thesis is to remark the significance of analyzing the sources of variability that may turn general laws into "less general" than they appear.

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CONCLUSIONS

Chapter 1

1. The population dynamics of wood mice were severely influenced by seasonal changes in the availability of a particular resource (acorns), resulting in a strong decline in survival probability, body mass and abundance during summer.
2. Space use by mice differed between males and females, owing to sexual differences in breeding behaviour.
3. Wild boars and shrub cover did not influence the demographic dynamics of wood mouse in the study area, as opposed to the findings in other habitats, highlighting the relevance of habitat structure in mediating rodent's performance.

Chapter 2

1. Wood mice responded to the different seeding phenology of *Quercus ilex* and *Q. pubescens* adapting their acorn preferences to the most abundant acorn species available on the ground.
2. The uncoupled phenology of *Quercus ilex* and *Q. pubescens* together with the plastic behaviour of mice removing seeds of the most abundant species, provide a window of chance for seed dispersal of both species, assisting in their coexistence.
3. The influence of seed size on wood mouse foraging choices showed a strong temporal consistence along the seeding season, suggesting that mice preference for larger seeds is a fixed behaviour.
4. The seed predation/dispersal remained constant with independence of the temporal variability in seed abundance and quality, revealing that wood mice are primarily seed removers.

Chapter 3

1. Wood mice responded to chemosensory information of predators and conspecifics changing their seed predation and dispersal behaviour accordingly.

2. Wood mice foraging in sites with predator scents displayed a more vigilant behaviour, whereas in sites with conspecific scent invested proportionally more time in gathering olfactory information (sniffing), suggesting a trade-off between anti-predatory behaviour and foraging efficiency when searching for food.
3. The removal of acorns from sites with predator scents was delayed, while removal from places with conspecific scent resulted in a reduced dispersal distance but also lower consumption rates of the seeds.
4. The dispersal patterns of acorns by wood mice, and the success of the seeds, may differ at a fine spatial scale in response to the scents of predators and conspecifics.
5. The influence of seed size in the preferences of mice was consistent along the different scent treatments, revealing that certain seed traits may strongly influence rodent's foraging decisions, regardless of the context.

Chapter 4

1. The spatial patterns of oak's recruitment was not affected by a nurse effect from shrubs in our dense-canopy forest, but was strongly promoted by acorn availability, and negatively affected by the pilferage activity of wood mice and the foraging activity of wild boars.
2. Besides their role as seed pilferers, wood mice also acted as seed dispersers, changing the seed shadows generated by trees dispersing acorns from under shrubs to open places, potentially contributing to seedling emergence and growth in the shady conditions of a closed-canopy forest.
3. Wood mice changed their seed dispersal behaviour influenced by the rooting activity of wild boars, increasing the consumption of acorns *in situ* instead of removing them to other sites.