

## Beyond predator satiation: Masting but also the effects of rainfall stochasticity on weevils drive acorn predation

JOSEP MARIA ESPELTA,<sup>1,†</sup> HAROLD ARIAS-LECLAIRE,<sup>1,2</sup> MARCOS FERNÁNDEZ-MARTÍNEZ,<sup>1,3</sup>  
ENRIQUE DOBLAS-MIRANDA,<sup>1</sup> ALBERTO MUÑOZ,<sup>4</sup> AND RAÚL BONAL<sup>5,6</sup>

<sup>1</sup>CREAF, Cerdanyola del Vallés, 08193 Catalonia, Spain

<sup>2</sup>Escuela de Ciencias Exactas y Naturales, Universidad Estatal a Distancia, Mercedes de Montes de Oca, San José 474-2050 Costa Rica

<sup>3</sup>CSIC, Global Ecology Unit, CREAM-CSIC-UAB, Cerdanyola del Vallés, 08193 Catalonia, Spain

<sup>4</sup>Departamento de Didáctica de las Ciencias Experimentales, Facultad de Educación, Universidad Complutense de Madrid, 28040 Madrid, Spain

<sup>5</sup>Forest Research Group, INDEHESA, University of Extremadura, 10600 Plasencia, Spain

<sup>6</sup>Grupo de Investigación de la Biodiversidad Genética y Cultural, Instituto de Investigación en Recursos Cinegéticos CSIC-UCLM-JCCM, 13005 Ciudad Real, Spain

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**Abstract.** Escaping seed predation is a classic “economy of scale” hypotheses (*predator satiation hypothesis, Psh*) to explain the selection for the synchronous production of massive and nil seed crops (masting) in plants. The *Psh* postulates that predator satiation occurs through a combination of (1) “functional satiation,” as not all seeds can be consumed during a massive crop, and (2) “numerical satiation,” as predator populations collapse during poor crop years. Many studies advocate for the *Psh*, but few have investigated the importance of masting compared to other factors for the control of predation extent. Namely, environmental cues prompting masting could also determine predator’s success and, ultimately, influence directly and independently seed predation intensity. We explored this question in Mediterranean oaks, as they exhibit strong masting behavior; acorns are heavily predated upon by weevils; and rainfall stochasticity drives masting and the emergence of adult weevils from the soil. Results of two mid-term studies (4 and 11 yr) showed that acorn production and predation were highly variable across years, while the abundance of adult weevils was positively related to autumn rainfall and to the number of infested acorns the previous years. Ultimately, acorn predation was negatively influenced by inter-annual fluctuation of seed production (masting) yet, mainly and positively, prompted by autumn rainfall and acorn crop size (only in one site). Our results highlight the relevance of masting to reduce seed predation. Yet evidences that rainfall stochasticity directly determines the success of weevils, and it independently influences seed predation extent, indicate that environmental cues prompting masting may also fine-tune the output of this reproductive behavior. Additionally, local differences suggest that the relevance of masting may change with tree characteristics (low vs. high seed production) and landscape structure (isolated vs. dense forests). We also discuss what can be the effects of increasing drought in Mediterranean areas for this antagonistic interaction, triggered by rainfall.

**Key words:** *Curculio* spp.; extended diapause; granivory; Mediterranean oak forests; plant–animal interactions; pre-dispersal seed predation; *Quercus ilex*; resource pulses.

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† **E-mail:** josep.espelta@uab.cat

## INTRODUCTION

The synchronous and intermittent production of large and nil seed crops (often termed *masting*) is a taxonomically and geographically widespread reproductive behavior among plants (Kelly and Sork 2002). The superabundance of seeds in certain years combined with periods of almost no reproduction not only influences the temporal patterns of seedling recruitment in these species (De Steven and Wright 2002, Oddou-Muratorio et al. 2011) but also results in an erratic pulse of resources triggering a cascade of “bottom-up” effects across trophic levels: seed consumers (Selva et al. 2012), predators of seed consumers (Ritchie and Johnson 2009), parasites (Jones et al. 1998), and even parasitoids (Satake et al. 2004).

Evolutionary hypotheses for the advantages of masting as a reproductive strategy are based on an “economy of scale” principle: A single but extraordinary reproductive episode should be more beneficial than continuous but moderate reproductive events (Kelly and Sork 2002). In this sense, the advantage of masting as a mechanism to reduce seed predation (*the seed predation satiation hypothesis* sensu Janzen 1971, see also Silvertown 1980) has probably been one of the hypotheses receiving greatest attention (Kelly et al. 2000, Yu et al. 2003, Espelta et al. 2008, Fukumoto and Kajimura 2011, Archibald et al. 2012, Moreira et al. 2017). As proposed by Satake et al. (2004), the synchronous, irregular production of large and nil seed crops would lead to predator satiation by combining two different mechanisms: (1) “functional satiation” (large seed crops surpass the feeding capacity of predators, see also Ims 1990) and (2) “numerical satiation” (the current number of predators may be too low to consume many seeds if the previous year’s crop was small, Bonal et al. 2012). Certainly, masting is expected to be especially effective in controlling predators with specialized seed-feeding habits, limited mobility, and a short life span encompassed within the seeding season (Shibata et al. 1998). This is the case of many preeminent seed consumers such as granivorous insects (e.g., weevils in Mulder et al. 2012, Muñoz et al. 2014, bruchids in Peguero et al. 2014).

Evidences of the benefits that extreme inter-annual variability in seed production may play

in reducing seed predation have been extensively suggested (Satake et al. 2004, Espelta et al. 2008, Peguero et al. 2014, Moreira et al. 2017). However, few studies have tested whether environmental factors (proximate causes) influencing masting might also be directly involved in controlling seed predator’s populations and thus also contribute to escape seed predation (but see Poncet et al. 2009). Therefore, while the relevance of environmental conditions for synchrony in reproduction and variability in seed crops has been thoroughly investigated (temperature in Schauber et al. 2002, Kelly et al. 2013, rainfall in Pérez-Ramos et al. 2010, Fernández-Martínez et al. 2015, or even “weather packages” in Fernández-Martínez et al. 2016, see also Koenig et al. 2016), their potential direct impact on the predators that consume these seeds has often been neglected. Temperature and precipitation may certainly have an effect on predation extent by determining food resource (crops) variability, but they may also directly influence the population size or the performance of seed consumers. For example, meteorological conditions are known to directly affect the population size and activity of rodents (e.g., squirrels in Kneip et al. 2011, wood mice in Wróbel and Bogdziewicz 2015, Sunyer et al. 2016) and ungulates (Servanty et al. 2009). Similarly, rainfall amount and its seasonal distribution may influence oviposition by granivorous insects (Bonal et al. 2010) by affecting the number of adults emerging from the soil (Schraer et al. 1998), or even altering their sex ratio (Bonal et al. 2015).

Disentangling the issue as to whether seed predation is mainly controlled by variability in seed production or by the direct impact of meteorological conditions on predators may help in shedding light on the evolution of this reproductive behavior in plants as well as to understand its relevance under new climatic scenarios arising from climate change. Mediterranean oaks (*Quercus* spp.) offer a worthwhile opportunity to examine this question since they show clear masting behavior (Koenig and Knops 2000) and acorns are largely consumed by seed predator specialists such as acorn weevils (*Curculio* spp.; Bonal et al. 2007). Moreover, rainfall stochasticity, including the occurrence of severe drought episodes, influence masting in these species (Espelta et al. 2008, Pérez-Ramos et al. 2010,

Fernández-Martínez et al. 2012) and the emergence of adult weevils from the soil after diapause (Bonal et al. 2010). Thus, the main aim of this study was to elucidate the contribution of the inter-annual variability in acorn crop size and the direct effects of precipitation (i.e., conditioning the likelihood of acorn weevil emergence from the soil) for the extent of acorn predation. To test this, we used an intensive four-year monitoring of acorn production, rainfall variability, adult weevil emergence from the soil after diapause, and acorn predation in isolated *Quercus ilex* trees in a savannah-like landscape, and also a database (11 yr) of acorn production, rainfall variability, and acorn predation by weevils in 15 forest stands. We specifically assessed (1) the inter-annual variability of acorn production and acorn predation, (2) the effect of rainfall on adult emergence from the soil and thus on the abundance of adult weevils, and (3) the dependence

of acorn predation rates on current crop size, inter-annual variability in acorn crop sizes, and rainfall amount, as a surrogate of the abundance of adult weevils. We hypothesize that, apart from the reported effects of rainfall stochasticity in determining masting in Mediterranean oaks (Espelta et al. 2008, Fernández-Martínez et al. 2012), it may play a relevant role in acorn infestation through its direct effect on the number of adult weevils present, thus fine-tuning the expected effects of masting on predation.

## MATERIALS AND METHODS

### Study area and species

This study was conducted in two different areas of Spain: Huecas (Toledo, central Spain) and Collserola (Barcelona, northeast Spain; Fig. 1) where the reproductive patterns of *Quercus ilex* and acorn predation by weevils (*Curculio*

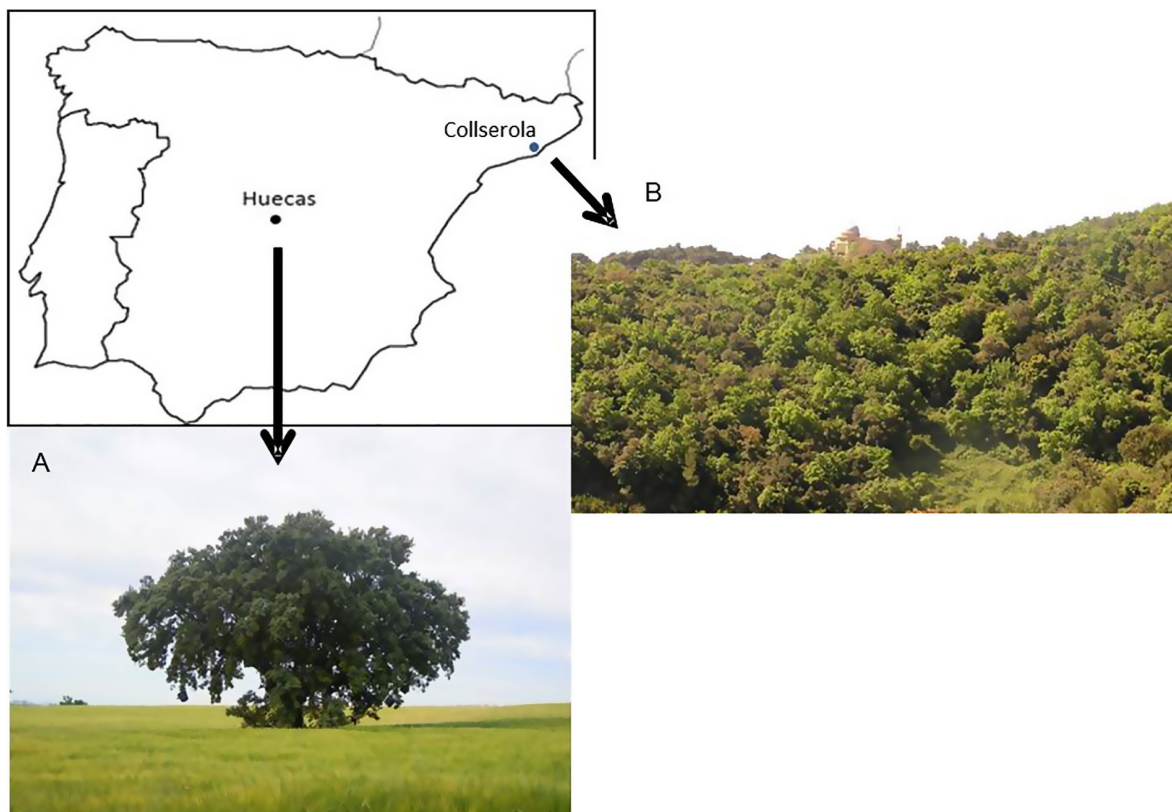


Fig. 1. Location of the study sites (Huecas and Collserola) in Peninsular Spain. Notice that Huecas (A) corresponds to a savannah-like landscape (“dehesa”) with scattered oaks, while Collserola (B) is an old-coppiced oak forest. Photograph A courtesy of Helena Ruíz-Carbayo.

spp.) have been thoroughly studied (Bonal et al. 2007, 2010, Espelta et al. 2008, 2009). Huecas is a savannah-like landscape with scattered *Q. ilex* trees (from 1 to 100 trees/ha, up to 2 km apart) embedded in a cropland matrix (Fig. 1A). Climate is continental Mediterranean with cold winters, extremely hot, dry summers, and rain concentrated in spring and autumn. Mean annual temperature ranges from 14.6° to 16°C, and mean annual precipitation ranges from 350 to 450 mm per year. The landscape structure allows the intensive monitoring of separate individual trees that are like “islands” for insects’ specialists on oaks (Ruíz-Carbayo et al. 2017). For the purpose of this study, we selected 24 focal trees and monitored acorn production and seed predation rates over four years (2009, 2010, 2011, and 2012) and adult weevil emergence from the soil beneath each tree over five years (2008, 2009, 2010, 2011, and 2012). Rainfall patterns from 2008 to 2012 were obtained from a local weather station. Collserola Natural Park is a coastal massif covered by dense, old-coppiced *Q. ilex* forests (see Fig. 1B). Climate is typically Mediterranean, with 614 mm of mean annual precipitation and monthly temperatures with a maximum of  $24.3^{\circ} \pm 0.7^{\circ}\text{C}$  in August and a minimum of  $8.5^{\circ} \pm 0.6^{\circ}\text{C}$  in January. Summer is the warmest, driest season, while most rainfall occurs in spring and autumn (Fernández-Martínez et al. 2012). For the purposes of this study, we used the data collected from 15 *Q. ilex* trees in 15 forest stands (~225 trees) where acorn production and seed predation were monitored from 1998 to 2009 (see Espelta et al. 2008 for methodological details). The annual pattern of rainfall per plot from 1998 to 2009 was obtained from the meteorological database developed in the MONTES project (M. Ninyerola and M. Batalla).

*Quercus ilex* acorns mature in one year and seed production is subjected to strong inter-annual fluctuations (Espelta et al. 2008). In Collserola, acorns are subjected to pre-dispersal predation by two weevil species, *Curculio glandium* and *Curculio elephas* (Espelta et al. 2009), while *C. elephas* is the prevalent acorn parasite in Huecas (Bonal et al. 2007). *Curculio glandium* is widely distributed in Europe associated with oak trees (*Quercus* spp.), while *C. elephas* is present in central and southern Europe, also associated with oaks (*Quercus* spp.) and chestnuts (*Castanea*

*sativa*). In the two study areas, both weevils can only infest acorns since there are no chestnuts around. Both *C. glandium* and *C. elephas* overwinter underground, but the two species present different phenologies: *C. glandium* emerges earlier, mostly in spring (Pélisson et al. 2013), while the emergence of *C. elephas* is restricted to autumn (Espelta et al. 2009, Bonal et al. 2012). After emerging, adult weevils climb to the crown for mating. This is the time when acorn predation also takes place (Bonal and Muñoz 2009, Espelta et al. 2009), after females drill a tiny hole in the seed cover with their rostrum and generally deposit a single egg in the developing acorn using their ovipositor. The two weevil species also differ in their dispersal ability and dormancy strategy. Adults of *C. glandium* emerge from the soil two years after larvae development and are able to fly up to 10 km, while *C. elephas* emerges in early autumn and has a much lower dispersal ability (Venner et al. 2011, Pélisson et al. 2013). In fact for *C. elephas*, genetic differences and restricted gene flow among populations are observed beyond 300 m (H. Ruiz-Carbayo, *unpublished manuscript*). This species also has the ability to spread the emergence of adults up to three years (~66% emerging the first year, 30% in the second, and 4% during the third year; see Venner et al. 2011, Pélisson et al. 2013).

#### Sampling design

In Huecas, acorns were collected using buckets (0.12 m<sup>2</sup> × 0.5 m) hung from the lower branches of every tree to prevent predation by large ungulates. The number of traps per tree was proportional to its canopy surface, and covered at least 1.5–2% of the canopy (see Bonal and Muñoz 2009 for details). Seed traps were sampled periodically and, after the first infested acorns were collected, traps were checked every 10 d until acorn fall ceased. On each revision, seeds were taken to the laboratory to identify sound and infested ones (Bonal and Muñoz 2009). In addition, to estimate the population size of acorn weevils and the phenology of their emergence from the ground, a survey of adult emergence was carried out from August 2008 to October 2012, using emergence traps attached to the trunks of focal trees. Each trap consisted of a cone of mosquito netting attached to the tree trunk with a closed bottle on top. After emerging from the soil, the weevils

climbed up the trunk and were trapped in the bottle (see Bonal et al. 2012 for further details). Distance between trees and their location in a hostile media for weevils (croplands) make successful dispersal of *C. elephas* among trees almost impossible (Bonal et al. 2012). Traps were checked on a daily basis from August to late October in order to record the number of individuals that had emerged. At the same time, weekly precipitation was measured at a local weather station for the same period in order to determine the possible influence of rainfall on the emergence of adults.

In Collserola Natural Park, acorn production and predation rates were recorded in 15 plots established in oak forests in 1998. At each plot, 15 trees were randomly selected (225 trees in total) from among those with most of their crowns exposed to full sun and with similar dbh. Each tree was tagged and four branches of similar size (~2–3 cm in diameter) were randomly chosen from different sections of the canopy (see Espelta et al. 2008 for further details). From 1998 to 2009, the number of acorns produced and infested was counted on these branches at the peak of the acorn crop in the area (usually in early to mid-September, Espelta et al. 2009). This sampling protocol was selected because the intermingling of tree branches precludes the possibility of individual monitoring of seed production per tree by means of seed traps (see Fig. 1B). Similarly, surveys of adult emergence were not conducted owing to the difficulties of performing them in these dense old-coppiced forests (~1500–2000 individuals/ha).

For each tree, we calculated the number of sound acorns produced per year, the number of parasited acorns, the inter-annual variability in acorn production (CV, coefficient of variation of seed production across years), and synchrony in the pattern of seed production. Synchrony was calculated as the Pearson's coefficient of correlation ( $r$ ) of non-log-transformed data of each tree with the rest of trees in Huecas and with all trees in the same plot in Collserola (see Espelta et al. 2008 for further details).

#### Data analysis

Generalized linear mixed models (GLMMs), following a binomial distribution, were used to test for the effects of several variables on acorn

predation rate (i.e., the ratio of infested acorns to the total number of acorns in year  $t$ ). Seed predation rate is the variable commonly used to investigate whether temporal variability in seed production (masting) may influence seed predation extent (see Satake et al. 2004, Bonal et al. 2007, Espelta et al. 2008, Moreira et al. 2017), as the use of the crude number of seeds depredated can be tightly linked to the number of seeds available. The rationale behind the inclusion of the different independent variables in the model and their expected impact (positive or negative) on acorn predation is listed below:

1. *Acorn crop size in year  $t$ .*—This variable may have a negative effect on predation if functional satiation takes place (Satake et al. 2004). Conversely, it could have a positive effect, especially in Collserola where the weevil with the highest dispersal ability is found (*C. glandium*), if weevils are attracted by more productive trees. Therefore, differences between the two study sites Huecas and Collserola may be expected due to their extremely different tree density.
2. *Number of infested acorns in year  $t-1$  and year  $t-2$ .*—The number of infested acorns during previous years can be assumed to be an estimate of the current size of the weevils' population in year  $t$ , especially if environmental conditions do not affect their success (no effects of rain). We added infested acorns in the previous two years, as the weevil species present both in Collserola and in Huecas (*C. elephas*) exhibits extended diapause (i.e., 96% of adults emerging in two years; Venner et al. 2011), and the other species present in Collserola (*C. glandium*) emerges after two years (Venner et al. 2011). This variable is expected to increase acorn predation (Bonal et al. 2010).
3. *Inter-annual fluctuation on seed production (i.e., ratio of mature acorn crop size in year  $t$  to that in year  $t-1$  and year  $t-2$ ).*—Inter-annual fluctuation in seed production is the variable often used to explore the potential advantages of masting for escaping seed predation by combining the numerical and functional satiation of predators (see Satake et al. 2004, Espelta et al. 2008, Tachiki and Iwasa 2013, Moreira et al. 2017). This variable is the ratio of the

size of the current acorn crop available to previous year crops, as the proxy of the potential number of adult weevils present in year  $t$ . This ratio is expected to be negatively related to acorn predation: A high ratio (a large acorn crop size in year  $t$  and a low seed production in previous years) would mean the presence of few adult weevils and a high number of acorns in year  $t$ , thus resulting in low predation rates.

4. *Rainfall*.—As rainfall amount is suggested to be a crucial factor to allow the emergence of adult weevils from the soil (Alverson et al. 1984), and this may directly affect acorn predation, we included in the analyses the values of total rainfall for the periods when the emergence of weevils has been observed in our study areas in previous studies: from September to October for *C. elephas* in Huecas and Collserola (Espelta et al. 2009, Bonal et al. 2010) and from May to June for *C. glandium* in Collserola (Espelta et al. 2009). In the two sites, we expected rainfall to have a positive effect on acorn predation as the greater the amount of rainfall, the more weevils would be able to emerge from the soil (Schraer et al. 1998) and potentially infest acorns.

The “plot” and the “tree” factors in Collserola and the “tree” factor in Huecas were included as random effects in the GLMM analyses to account for the repeated nature of the measurements and other unexplained variation. Selection of the most adequate model was done by using the dredge function of the MuMIn package in R (Barton 2015). Comparison of sets of alternative models was done by using differences in the second-order (or corrected) Akaike Information Criterion ( $AIC_c$ ) and contrasting models by using  $\chi^2$  tests. Inclusion of a variable in the model required a significant  $\chi^2$  test ( $P = 0.05$ ) and a difference between  $AIC_{cs}$  (delta:  $\Delta AIC_c$ ) of at least of four units compared to the same model excluding that variable. Pseudo-coefficients of determination ( $R^2$ ) were used to estimate the contribution (in %) of fixed effects ( $R^2_{\text{marginal}}$ ) and both fixed and random effects ( $R^2_{\text{conditional}}$ ) in explaining the variability of acorn predation.

To test for the main factors accounting for the abundance of adult weevils in a given year in the

site where we monitored their emergence (Huecas), we ran a GLM including the number of weevils emerging per tree and year as the dependent variable and rainfall during the season of emergence (from September to October) and the number of acorns infested during year $_{t-1}$  and year $_{t-2}$  per tree as the independent factors. In addition, we analyzed the relationship between rainfall and emergence of adult weevils from the soil at a fine-grained temporal scale by plotting the number of emerged weevils and the amount of rainfall per week. We then ran correlation analyses comparing rainfall accumulated in one or two weeks and the number of emerged weevils one week later, since a minimum rainfall threshold is needed to soften the soil enough for weevil emergence (Mulder et al. 2012 and references therein).

Data analyses were performed using the R statistical software program, version 3.1.1 (R Development Core Team 2014).

## RESULTS

Annual acorn production varied in both study sites with years of abundant and low seed crops, although this pattern was much more evident in Collserola than in Huecas (Fig. 2,  $CV = 1.97 \pm 0.07$  in Collserola and  $0.94 \pm 0.11$  in Huecas). In Collserola, oaks usually exhibited very low acorn production ( $422 \pm 139$  acorns·tree $^{-1}$ ·yr $^{-1}$ ), and there were high pulses of production in only three out of 11 yr (Fig. 2A): remarkable peaks in 2002, 2004, and 2008 and almost no mature acorn production in 2000, 2001, and 2005. In Huecas, trees were more productive ( $5281 \pm 1608$  acorns·tree $^{-1}$ ·yr $^{-1}$ ), yet similar to Collserola, and despite a shorter time series, there was a year with a remarkable crop size (2012) preceded by some with lower values (Fig. 2B). Synchrony among trees in their inter-annual pattern of seed production was also higher in Collserola than in Huecas (Pearson's  $r$ :  $0.67 \pm 0.05$  and  $0.36 \pm 0.09$ , respectively). Parallel to the large variation observed in seed production, the proportion of acorns depredated by weevils exhibited large variability over the years in both sites, with a pattern of low values in years of high seed production and more variable rates (both low and high) in years of lower acorn crops (Fig. 2). In Collserola, the higher predation rates were observed in 2001, 2003, 2006, and 2009 as opposed to 2000,

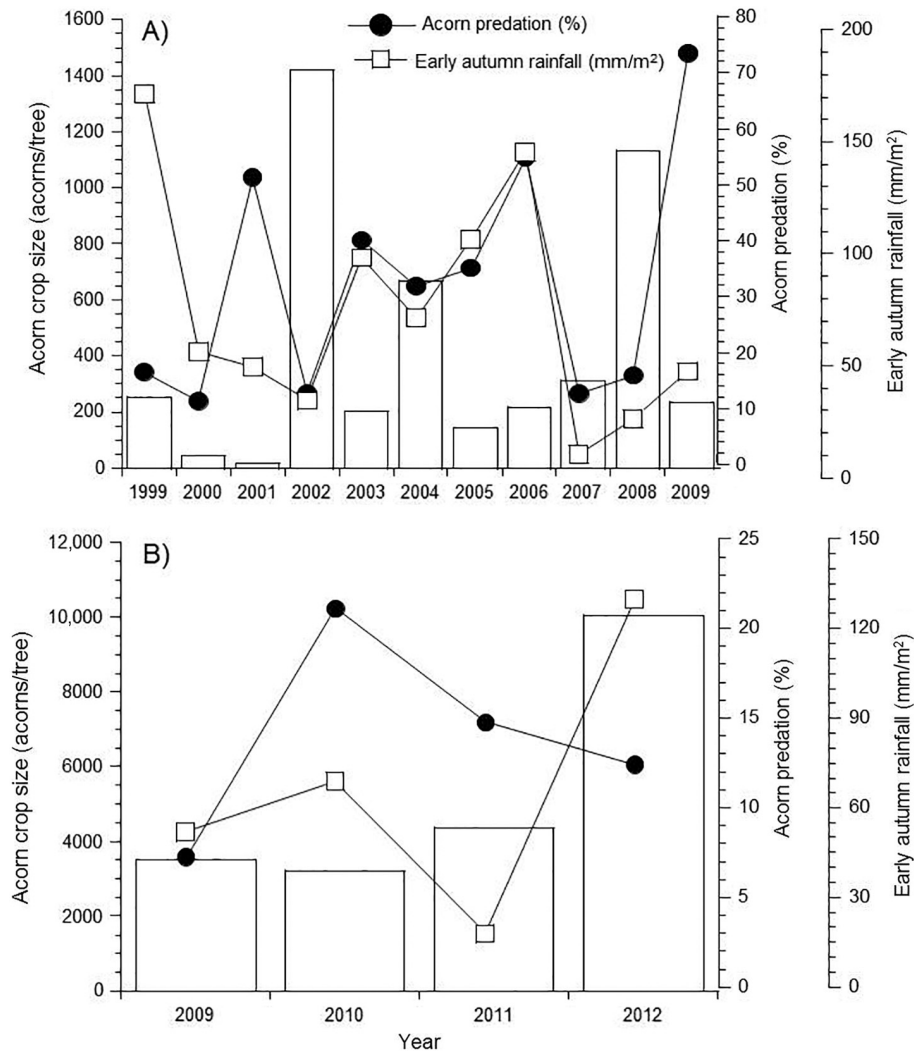


Fig. 2. Mean acorn production per tree (columns), mean acorn predation percentage per tree (black dots), and cumulative rainfall (empty squares) in early autumn (September and October) in Collserola (A) and Huecas (B).

2002, and 2007 (Fig. 2A), while in Huecas (Fig. 2B) 2009 and 2012 showed lower predation rates than 2010 and 2011.

The detailed (“per tree”) monitoring of adult weevil emergence conducted in Huecas revealed that the number of adult weevils present in a given year was significantly and positively related to the amount of autumn rainfall that year ( $F = 12.61$ ,  $P < 0.001$ ) and to the number of infested acorns—a proxy of the number of larvae—the two previous years ( $F = 24.9$ ,  $P < 0.001$ ). This relationship between the numbers of adult weevils present (emerged from the soil) and

rainfall amount in early autumn is also supported by the weekly patterns of rain accumulated and the number of weevils emerged and trapped (Fig. 3). In the four years included in the study, emergence of adult weevils from the soil started in early September and peaked some weeks later, roughly at the end of October, concurrent with rainfall accumulation patterns (see Fig. 3). In fact, emergence was positively correlated ( $r = 0.53$ ,  $P < 0.001$ ) with the amount of rainfall in the previous two weeks, probably because some time is needed to moisten and soften the soil enough to facilitate the emergence process.

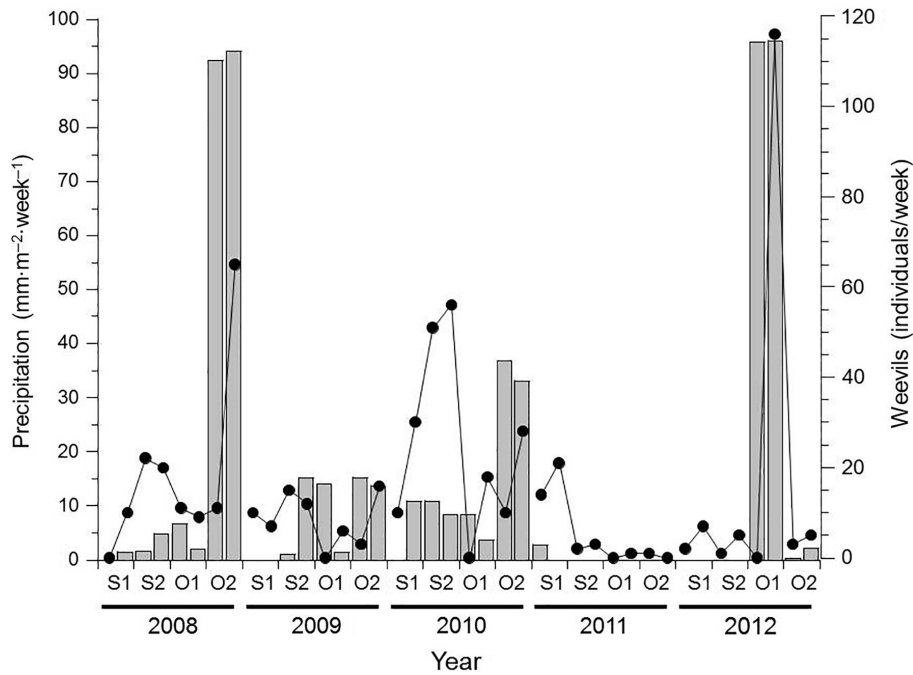


Fig. 3. Weekly precipitation (gray columns) and adult weevil emergence (black dots) from early September to late October for the years 2008 to 2012 in Huecas. S = September; O = October; 1 = first half month; 2 = second half month.

As shown in Table 1, in Collserola, acorn predation per tree was significantly influenced by the size of the current acorn crop, rainfall amount in early autumn, and inter-annual fluctuation of

seed production (ratio of acorn crop  $t$  to acorn crop  $t-1$  and  $t-2$ ). In the model, acorn crop size and autumn rainfall had a positive effect on acorn predation, while inter-annual fluctuation in seed production (masting) had a negative effect. Similarly, in Huecas, the proportion of infested acorns per tree was significantly affected by inter-annual fluctuation in seed production and by autumn precipitation (Table 1). As observed in Collserola, rainfall had a positive effect on acorn predation, while inter-annual fluctuation had a negative effect (Table 1). In both sites, considering the relative importance of all variables included in the model, early autumn rainfall was the main source of acorn predation variability followed by inter-annual fluctuation in seed production (see Table 2 and also Fig. 2 for the similarity in the patterns of early autumn rainfall amount and acorn predation).

Table 1. Coefficients of the significant effects in the generalized linear mixed models on the effects of crop size $_t$ , crop size $_{t-1}$  and  $t-2$ , inter-annual variability in crop size (ratio of crop year $_t$  to crop year $_{t-1}$  and  $t-2$  hereafter crop ratio), autumn rainfall, and spring rainfall on acorn predation rate per tree in year  $t$  (see the Data analysis section for further details about these variables).

Site	Effect	Estimate	Std. error	z-Value
Huecas	Intercept	-0.56682	0.16953	3.277**
	A. Rainfall	1.02438	0.14032	7.155***
	Crop ratio	-0.44428	0.14161	3.075**
Collserola	Intercept	-3.9772	0.2330	16.091***
	Crop $_t$	0.7540	0.2210	3.284***
	A. Rainfall	1.8931	0.2617	6.915***
	Crop ratio	-1.3791	0.2687	5.572***

Notes: A. rainfall, autumn rainfall. Predictors are ordered by relative importance established by the dredging process according to maximum likelihood and the model average function.  
<sup>\*</sup> $P < 0.05$ , <sup>\*\*</sup> $P < 0.01$ , and <sup>\*\*\*</sup> $P < 0.001$ .

### DISCUSSION

Our results demonstrate that early autumn rainfall stochasticity directly affects the emergence of adult weevils from the soil, and this



Table 2. Relative contribution of the different variables explaining acorn predation calculated by comparing the best model and alternative models with an identical fixed-effects structure, but ignoring one variable at a time.

Site	Model	df <sub>mod.</sub>	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	df <sub>test</sub>	χ <sup>2</sup>	R <sup>2</sup>	
							Marg.	Condit.
Huecas	Best model	6	374.3				0.205	0.385
	A. Rainfall	4	408.6	34.2	2	39.0***	0.015	0.398
	Crop ratio	4	378.7	4.4	2	9.1*	0.175	0.395
Collserola	Best model	8	6417.3				0.167	0.910
	A. Rainfall	6	6504.2	68.9	2	74.0***	0.068	0.900
	Crop ratio	6	6495.5	33.1	2	37.2***	0.123	0.912
	Crop <sub>t</sub>	7	6437.7	9.3	1	10.9***	0.152	0.903

Note: df<sub>mod.</sub>: degrees of freedom of the model; df<sub>test</sub>: degrees of freedom of the test; marg.: marginal R<sup>2</sup>, proportion of variance explained by the fixed factors alone; condit: conditional R<sup>2</sup>, proportion of variance explained by both the fixed and random factors; AIC<sub>c</sub>, Akaike Information Criterion.

\*P < 0.05, \*\*P < 0.01, and \*\*\*P < 0.001.

effect may become as important as the inter-annual variation in acorn crop size (masting) for acorn predation extent. Interestingly, as masting in Mediterranean oaks is also driven by inter-annual differences in rainfall amount, mostly in spring and summer (see Espelta et al. 2008, Fernández-Martínez et al. 2012, 2015, Koenig et al. 2016), rainfall stochasticity appears as the trigger point of this complex plant–animal interaction and its final outcome: acorn predation. Indeed, our results do not falsify the predator satiation hypothesis as an ultimate cause for the selection of masting. Yet they highlight that proximate environmental causes involved in this reproductive phenomenon may also directly and independently influence seed predation extent, thus fine-tuning the effects of inter-annual seed variability. To what extent this role may change under new ecological scenarios arising from climate change (e.g., increasing drought in Mediterranean areas) remains a challenging question to be further investigated.

Early autumn rainfall influenced the emergence of adults of *Curculio elephas* from the soil, and this is the most likely explanation for the positive influence of precipitation during this season on acorn predation extent. Previous studies, both experimental (Alverson et al. 1984, Schraer et al. 1998) and observational (Bonal et al. 2010), had already shown a positive relationship between precipitation and adult weevil abundance, with the need of a certain rainfall amount threshold to enhance their emergence (Fig. 3, see also Mulder et al. 2012). Yet for the first time, we demonstrate that this effect may

influence seed predation extent. Rainfall in early autumn certainly would benefit the emergence of *C. elephas*, the weevil with a later phenology, and the only one present in Huecas, but not *Curculio glandium*, the second species present in Collserola that emerges in spring. The lack of significant effects of spring rainfall we observed for acorn predation in this site may be due to the fact that moister conditions during late winter and initial spring observed in the soils of the study area (Sánchez-Costa et al. 2015) make rainfall not to be such a crucial factor for the emergence of *C. glandium* as it is for *C. elephas* after summer.

The effect of rainfall stochasticity on the emergence of some weevil species becomes crucial to explain why predation rates do not always match the *functional* and *numerical satiation* effects presumably associated with inter-annual crop variability. For example, as shown in Fig. 2A, acorn predation in Collserola in 2007 was as low as the values observed during the two masting events (2002 and 2008), although the crop size in 2007 was much lower (poor *functional satiation* expected) and very similar to that of the previous year 2006 (poor *numerical satiation* expected). Interestingly, in 2007, rainfall in September–October was extremely low (Fig. 2A) and this could constrain weevil emergence from the soil and reduce predation intensity. Similarly, in Huecas, predation in 2011 was much lower than that in 2010, even though the number of acorns produced in these two years was very similar (Fig. 2B), probably owing to the extremely dry autumn in 2011 (see Fig. 3).

Our results demonstrate that aside from acorns, weevils require perform a certain amount of

rainfall at a very precise time of the year (autumn) in order to be able to emerge from the soil and successfully infest the acorns. Interestingly, this environmental requirement is uncoupled with the ones driving acorn production as this mostly depends on rainfall in spring and early summer (Espelta et al. 2008, Fernández-Martínez et al. 2012, 2015), with barely any effects of autumn rain, when acorns have almost fully developed (Espelta et al. 2009). Therefore, in a year with a large acorn crop available after optimal conditions in spring and summer, weevils could not benefit from it, if a dry autumn occurs and it blocks their emergence. This suggests that extended diapause in weevils is indeed a complex phenomenon that might have evolved not only to cope with the extreme inter-annual variability in seed crop size but also to cope with the effects of climate uncertainty (see also Venner et al. 2011, Pélişson et al. 2013). At the same time, it is challenging whether masting promoted variable diapause or it was the unpredictable emergence of weevil adults, prompted by rainfall stochasticity, what made masting advantageous for oaks. In any case, theoretical models developed by Satake and Bjørnstad (2004) suggest that, whatever the origin for extended diapause in a predator, extremely high temporal variability in seed production (masting) would benefit the host to buffer its effects.

The relevance of rainfall for controlling seed predation by weevils also challenges which will be the outcome of this antagonistic interaction in new climatic scenarios arising from climate change. In Mediterranean-type areas, the predicted increase in the intensity and length of drought events will certainly affect the patterns of acorn production, reducing the size of acorn crops, as has been already tested in experiments of rainfall exclusion (Sánchez-Humanes and Espelta 2011). Yet extended drought may also directly affect weevil populations by limiting the success of their emergence (Bonal et al. 2010) or even altering the sex ratio of populations (Bonal et al. 2015). This raises the question as to whether inter-annual variability in seed production or direct rainfall shortage effects on weevils will increase in importance for controlling acorn predation as climate change progresses (see also McKone et al. 1998, Poncet et al. 2009).

The observed effect of inter-annual crop variability to reduce acorn predation supports

*predator satiation* as one of the evolutionary hypotheses based on a plant–animal interaction to explain masting in oaks. Certainly, it could be argued that there are other animals also feeding on acorns such as rodents, birds, or ungulates not included in this study. However, weevils are one of the most important pre-dispersal acorn consumers, being able to destroy up to 60% of the crop in a given year (Leiva and Fernández-Alés 2005), and the only ones that comply with the three characteristics suggested by Shibata et al. (1998) to make a predator highly sensitive to inter-annual seed variability: short life span, reduced mobility, and high specificity. In addition to these effects, we cannot discard that the production of extraordinary large crops may also increase the chances of successful seed dispersal and recruitment in these species both by increasing the attraction of avian seed dispersers (Pesendorfer and Koenig 2016) and by reducing the removal of cached seeds during masting years (dispersal satiation hypothesis in vander Wall 2010, see also Zwolak et al. 2016).

In contrast to some previous studies, we did not observe a higher proportion of seeds consumed at low levels of seed availability, the so-called type II functional response of seed consumers (sensu Holling 1959, see also Moreira et al. 2017), indicating that the effects of masting may be somewhat idiosyncratic. In fact, although the effects of masting and early autumn rain on acorn predation were similar in the two localities, they differed in the intensity of these effects and the importance of other variables: greater importance of masting in Collserola and of rainfall in Huecas and significant effect of the current acorn crop sizes in the former site (see Tables 1 and 2). Moreover, in Collserola, the high value of the  $R^2$  conditional (~0.90), which accounts for the variability explained by random factors, suggests a major importance of the factor “plot” that may be due, among others, to differences in acorn production among forest stands (see also Espelta et al. 2008). Considering the size of crops produced in the two sites, it seems reasonable that masting had more importance in a site like Collserola where trees produce smaller crops (~10% of the values recorded in Huecas, see Fig. 1 and Espelta et al. 2008), forests are more continuous, and adult weevils of *C. glandium* are much more able to disperse from one tree to another. The

production of moderate-low seed crops and the intermingling of trees may explain why weevils disperse and may concentrate on relatively more productive trees, a pattern suggested by the positive effect we observed of the current acorn crop size on predation (Table 1). This scenario would give masting a greater importance to control seed predation (see also Maeto and Ozaki 2003). Conversely, isolated trees in the savannah-like landscape of Huecas are bigger, less resource limited, and may produce larger acorn crops regularly (Morán-López et al. 2016). In this situation, although masting remains still important, the direct effects of rainfall stochasticity on weevils may become more relevant to control acorn predation extent. Altogether, these local differences suggest that the relevance of masting may be somewhat context dependent and change with the size and productivity of trees and the landscape structure (see also Espelta et al. 2008, Yamauchi et al. 2013), especially in long-lived tree species such as oaks, a question that has been barely addressed up to now and requires further research.

## CONCLUSION

The main contribution of our study has been to demonstrate that irregular seed crops (masting) certainly help escaping acorn predation in Mediterranean oaks, yet the direct effects of rainfall stochasticity on the success of weevil populations may be as important as in reducing seed predation extent. Furthermore, our results suggest that the importance of masting to mitigate seed predation may change with individual characteristics (e.g., seed production) and spatial attributes (i.e., isolation). Our findings also question whether the increase in more severe and long-lasting drought events in Mediterranean areas owing to climate change will have a positive or negative impact in the outcome of this plant–animal interaction.

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