

1 **Biological integrity enhances the qualitative effectiveness of conditional mice-oak**  
2 **mutualisms**

3 **Teresa Morán-López<sup>1</sup>, Jesús Sánchez-Dávila<sup>2</sup>, Ignasi Torre<sup>3</sup>, Alvaro Navarro-**  
4 **Castilla<sup>4</sup>, Isabel Barja<sup>4,5</sup>, Mario Díaz<sup>2\*</sup>**

5 **1** Laboratorio Ecotono, INIBIOMA-CONICET, Universidad Nacional del Comahue,  
6 Black River, Argentina, **2** Department of Biogeography and Global Change (BGC-  
7 MNCN-CSIC), National Museum of Natural Sciences, CSIC, c/Serrano 155bis, E-  
8 28006 Madrid, Spain, **3** Museu de Ciències Naturals de Granollers (MCNG), E-08402  
9 Granollers, Barcelona, Spain, **4** Departament de Biologia, Unit of Zoology, Faculty of  
10 Sciences, Universidad Autónoma de Madrid, C/Darwin 2, Campus Universitario de  
11 Cantoblanco, 28049 Madrid, Spain, **5** Centro de Investigación en Biodiversidad y  
12 Cambio Global (CIBC-UAM) Universidad Autónoma de Madrid, C. Darwin 2, E-28049  
13 Madrid, Spain

14

15 *\* Correspondence: E-mail [Mario.Diaz@ccma.csic.es](mailto:Mario.Diaz@ccma.csic.es); tel +34 91 782 21 02; fax +34*  
16 *91 564 08 00*

17

18 Running headline: Predation and competition unbalance mice-oak conditional  
19 mutualisms

20

21 Word count: abstract: 241; main text: 3646; 65 references, 2 tables, 3 figures, 5

22 Supplementary files

23 Abstract

24 Scatter-hoarding decisions by rodents are key for the long-term maintenance of  
25 scattered tree populations. Decisions are determined by seed value, competition and  
26 predation risk, so that they can be influenced by the integrity of the biological system  
27 composed by trees, rodents, ungulate competitors, and rodent predators. We manipulate  
28 and model the oak-mice interaction in a Spanish dehesa, an anthropogenic savanna  
29 system suffering chronic tree regeneration failure, and quantify the joint effect of  
30 intrinsic and extrinsic factors on acorn dispersal effectiveness. First, we conducted a  
31 large-scale cafeteria field experiment, where we modified ungulate presence and  
32 predation risk, and followed mouse scatter-hoarding decisions under contrasting levels  
33 of moonlight and acorn availability. Then, we estimated the net effects of competition  
34 and risk by means of transition probability models that simulated mouse scatter-  
35 hoarding decisions according to the environmental context. Our results show that  
36 suboptimal conditions for mice balance the interaction towards the mutualism as they  
37 force mice to forage less efficiently. Under stressful conditions (predation risks and  
38 presence of ungulates), lack of antipredatory cover around dehesa trees limited  
39 transportation of acorns, but also precluded mice activities outside tree canopies. As a  
40 result, post-dispersal predation rates were reduced and large acorns had a higher  
41 probability to survive. Our work shows that inter-specific interactions preventing  
42 efficient foraging by scatter-hoarders benefitted seed dispersal. Therefore, the  
43 maintenance of the full set of producers, consumers, dispersers and predators in  
44 ecosystems is key for promoting seed dispersal effectiveness in conditional mutualisms.

45 *Keywords:* synzoochory, scatter-hoarding, competition, risk, seed fate

## 47 **Introduction**

48 Scatter-hoarders are key dispersers in temperate and Mediterranean forests where acorn-  
49 bearing trees (oaks) tend to be dominant [1-5]. Nut dispersal by scatter-hoarders  
50 (synzoochory) is a classical plant-animal conditional mutualism. The outcome of the  
51 interaction may be either mutualistic (dispersal) or antagonistic (predation) depending  
52 on whether seeds are consumed or, alternatively, cached and not retrieved [6]. The  
53 balance between mutualism and antagonism is contingent on intrinsic properties of  
54 interaction partners (e.g. propensity of animals to store food) as well as on the  
55 ecological setting in which the interaction occurs [5]. As a result, the net effects of  
56 synzoochory can be highly dynamic in space and time making difficult to predict its  
57 outcomes along environmental gradients and ecological timescales [7, 8].

58 Several mice species (*Apodemus*, *Mus*, *Peromyscus*) are the main scatter-hoarders in  
59 landscapes where avian dispersers (corvids; [9]) are absent, scarce or inefficient [2, 10].  
60 Two main external factors modulate mouse scatter-hoarding decisions: competition for  
61 seeds and predation risks [11-13]. Intraspecific competition and the presence of  
62 ungulates tend to encourage seed mobilization [6, 14-16]. Especially, when predating  
63 seeds *in situ* is more time-consuming than storing them for later consumption [12] and  
64 shrubs provide enough antipredatory cover during transportation [16, 17]. Even though  
65 lack of antipredatory cover can limit dispersal [16], intermediate risks can promote  
66 mobilization when mice carry away seeds to manipulate them in safer locations [12].  
67 Risk perception, in turn, depends on factors that affect exposure to predators (e.g.  
68 moonlight) and direct cues of their presence (e.g. scent) [19-24]. Overall, moderate level  
69 of stress for foraging mice (i.e. competition and predation risk) tend to unbalance the  
70 rodent-tree interaction towards its mutualistic side. In the absence of stress, rodents

71 usually act as efficient seed predators consuming, immediately or soon afterwards, seed  
72 crops under the canopy of mother trees [5].

73 Beyond the environmental conditions of plant-animal encounters, seed size can affect  
74 the initial outcomes of the interaction (selected, eaten or cached) as well as post-  
75 dispersal processes such as germination and seedling survival. Larger seeds are usually  
76 selected and preferentially cached because they provide higher food rewards [3, 24-28].  
77 In addition, seed size enhances post-dispersal seedling survival and establishment [29],  
78 which is a key component of dispersal effectiveness [30] in scatter-hoarder animals [3,  
79 5, 31]. Nonetheless, the strength and even sign of acorn size effects on mouse foraging  
80 decisions are not unequivocal, but context-dependent. Larger acorns are most preferred  
81 when food is scarce [32-34], but may be avoided when longer handling times [27]  
82 diminish their profitability [35, 36] or result in unaffordable predation risks during  
83 manipulation [11, 12]. Therefore, a full picture of the location of mice in the  
84 antagonism-mutualism continuum [4] requires accounting for seed size effects on  
85 scatter-hoarding decisions as well as the influence of competition and risk.

86 In this context, dehesas represent an excellent study system to assess the main factors  
87 modulating mouse foraging decisions, and hence, dispersal. They are savanna-like  
88 habitats, simpler than natural forests but diverse enough to maintain all key elements  
89 influencing the oak-mice conditional mutualism. In spite of this, dehesas, as well as  
90 other man-made systems dominated by scattered trees, suffer from a chronic lack of tree  
91 regeneration that compromises its long-term sustainability [37, 38]. Depending on the  
92 local intensity of management, nearby areas can have contrasting levels of shrub cover,  
93 mice densities and competition with ungulates [39, 40]. In addition, the community of  
94 predators is simpler than in forest areas, facilitating the experimental manipulation of  
95 direct cues of risks [24]. In this work we take advantage of a large-scale experiment of

96 ungulate enclosure in a Mediterranean dehesa to (1) quantify acorn size effects across  
97 different stages of the dispersal process (from seed choices to initial fates); and (2)  
98 evaluate if size effects are consistent across contrasting scenarios of predation risk and  
99 inter- and intraspecific competition. In addition, we parameterized a transition  
100 probability model that assembled all scatter-hoarding decisions by mice to quantify and  
101 tease apart the net effect of competition and risk on acorn dispersal. Our integrated  
102 approach combining field experiments and mechanistic modelling will allow testing  
103 whether the key role of rodents as seed dispersers in scattered tree systems can be  
104 enhanced by restoring the biological integrity of these systems [13].

105

## 106 **Methods**

### 107 **Study area and species**

108 Field work was carried out in the holm oak *Quercus ilex* dehesa woodlands of the  
109 Cabañeros National Park (Central Spain, Ciudad Real province, 39°24' N, 38°35' W).  
110 Dehesas are savanna-like man-made habitats resulting from shrub removal and tree  
111 thinning and pruning to enhance herb growth for livestock [41]. The studied dehesas  
112 were opened in the late 1950s. Currently they have no livestock but wild ungulate  
113 populations of red deer *Cervus elaphus* and wild boars *Sus scrofa*. Deer densities were  
114 around 0.14 ind./ha [42] and boars are abundant but at unknown densities [43]. Acorns  
115 fall from trees from mid-October to late November [44].  
116 The study area covers around 780 ha, with two ungulate enclosures (made with wire  
117 fences 2 m tall and 32 cm x 16 cm mesh) of 150 ha and 4.65 ha separated from each  
118 other by 1500 m. The enclosures prevent the entrance of ungulates but not of  
119 mesocarnivores (mainly common genets *Genetta genetta* and red foxes *Vulpes vulpes*;  
120 pers. obs. based on scat searches) and raptors. Both areas have similar tree abundance

121 (average density 20.4 trees ha<sup>-1</sup>) and low shrub cover (<1%), as measured on aerial  
122 photographs and vegetation surveys both under canopies and outside them [24]. The  
123 Algerian mouse is the most abundant scatter-hoarding rodent in the area [45], and it is a  
124 common prey of genets and other generalist predators [46, 47].

125

## 126 **Experimental design**

127 Tree occupancy by mice was established by means of live trapping using Sherman traps  
128 (23 × 7.5 × 9 cm; Sherman Co., Tallahassee, USA) baited with canned tuna in olive oil  
129 mixed with flour and a piece of apple. Water-repellent cotton was provided to prevent  
130 the cooling of the individual captured overnight. Traps were set during two consecutive  
131 days during the new moon of January 2012. High capture probability of *M. spretus*  
132 (detectability: 0.88±0.03SE; [48]) allowed to consider false negatives in occupancy  
133 unlikely. Among trees known to be occupied by Algerian mice, we randomly selected  
134 ten trees inside and ten outside in each of the two exclosures (40 focal trees in total).

135 We paired focal trees according to their proximity and we randomly assigned a predator  
136 scent treatment to one of them. Predator scent treatment consisted in placing fresh genet  
137 feces (10 g) mixed with distilled water close to a corner of the cages where acorns were  
138 placed [24]. Genets are generalist predators whose presence and scats are known to  
139 influence rodent behavior [17, 21, 23]. Fresh feces were collected from two captive  
140 common genets housed in the Cañada Real Open Center (Madrid, Spain).

141 Fresh acorns were collected from holm oaks growing near the study area in October  
142 2011 and stored dry in a cooler (4 °C) until use. Sound acorns, with no marks of insect  
143 damage [45], were weighed with a digital balance to the nearest 0.01 g. Groups of 15  
144 acorns in three categories were randomly selected (5 each, large, >10 g; medium-sized,  
145 5-10 g, and small, 1-5 g). Acorns were placed under the canopy of each focal tree inside

146 a 50 cm × 50 cm x 15 cm galvanized-steel cage to prevent acorn consumption by birds  
147 or ungulates [45]. A metal wire ( $\varnothing$  0.6 mm, 0.5 m length) with a numbered plastic tag  
148 was attached to each acorn [16]. After removing any naturally-present acorn within the  
149 cages, we randomly placed acorns in the intersection of a 3 rows x 5 columns grid. To  
150 track mouse choices, acorn size for each position was noted. Acorns were left exposed  
151 to mice for three consecutive nights, then removed. Mobilized acorns were located by  
152 looking at the plastic tags during the following days. To account for changes in night  
153 brightness and acorn availability [19, 22], the cafeteria experiment was repeated four  
154 times during the full-moon and new-moon periods of November 2011 and February  
155 2012. No official permits or protocol approvals were legally necessary since we did not  
156 manipulate individual mice except for checking whether trees were occupied or not by  
157 means of live traps. We followed Guidelines of the American Society of Mammalogists  
158 for the use of wild mammals in research [49]. We performed all manipulations with  
159 disposable latex gloves, to avoid effects of human odor on rodent behavior [50].

160

### 161 **Mouse foraging behavior**

162 A video-camera OmniVision CMOS 380 LTV (OmniVision, Santa Clara, USA) (3.6  
163 mm lens) monitored mice foraging activity within each cage [17]. Cameras were set on  
164 1.5 m tall tripods located 2.5 m from each cage, powered by car batteries (70 Ah, lead  
165 acid) connected to a solar panel (mono-silicon erial P\_20; 20 w). Video-cameras were  
166 connected to ELRO recorders with dvr32cards (ELRO, Amsterdam, Netherlands) and  
167 took continuous record for three consecutive days autonomously (recorded in quality at  
168 5 frames s<sup>-1</sup>). Events with rodent activity, from the entry of the individual into the cage  
169 up to the exit from it, were located and separated using Boilsoft Video Splitter software  
170 (<https://www.boilsoft.com/videosplitter/>)[17]. Within each event we noted which acorn

171 was manipulated and whether it was removed outside the cage. For removed acorns we  
172 measured mobilization distance (cm) and noted its status (predated or not after  
173 transportation).

174

## 175 **Data analysis**

176 To assess acorn choice by rodents, we fitted a hierarchical multinomial model. Our  
177 response variable was acorn selection (yes/no). Our explanatory variables were: acorn  
178 size (g), moon phase (new/full), month (February, November), ungulate presence  
179 (yes/no), predator scent (yes/no), acorn availability in the cage (g) and the two-way  
180 interactions between size and environmental effects. Local acorn availability was  
181 measured as total acorn mass in the cage during the event. Both, acorn size and  
182 availability were scaled previous to the analyses. Focal tree was introduced as a random  
183 factor in the intercept term. To evaluate the effects of acorn size on the probability of  
184 removal, we used a hierarchical logistic model. Our response variable was whether a  
185 selected acorn was mobilized outside the cage or not (yes/no). Our explanatory  
186 variables and random effects were the same as in the multinomial model.

187 Subsequently, we analyzed the effect of acorn size and environmental covariates (and  
188 their two-way interaction) on seed dispersal. Our response variables were mobilization  
189 distances (cm, log-transformed) and deposition status (viable or predated). We used a  
190 hierarchical Gaussian model in the former case, and a hierarchical logistic model in the  
191 latter. Our explanatory variables and random effects were the same as in the previous  
192 models. In all four models (selection, removal, mobilization distance and fate) we used  
193 uninformative priors (Supplementary File 1). All analyses were performed employing a  
194 Bayesian approach with JAGS 3.4.0 [51]. We checked for convergence for all model  
195 parameters ( $R_{hat} < 1.1$ ) and that the effective sample size of posterior distributions was



196 high (>800). We estimated mean and credible interval of posterior distributions,  
197 calculated the proportion of the posterior distribution with same sign of the mean (f) and  
198 evaluated the predictive power of our models by means of posterior predictive checks  
199 (Supplementary Files 1 and 2).

200

### 201 **Simulating scatter-hoarding decisions**

202 To estimate the joint effect of seed size, competition and risk on acorn dispersal we  
203 designed a probability transition model in which simulated mice adapted their foraging  
204 behavior to the environmental context (Supplementary File 3). Before model run, we  
205 parameterized mouse scatter-hoarding decisions (from selection to initial fate) following  
206 the same scheme of regressions explained in the previous section. Nonetheless, here we  
207 only used data from November, the period of peak acorn falling in our study system.  
208 Consequently, we did not include month as a covariate. For each behavioral submodel  
209 (selection, removal and initial fate), we obtained posterior distributions of parameters by  
210 running 50000 iterations in three chains (in all cases  $R_{hat} < 1.1$ , and  $N_{eff} > 1000$ ).

211 Model setup mimics our experimental design, 20 trees outside and 20 inside exclosures  
212 paired according to a predator scent treatment (presence vs. absence). Simulations begin  
213 under new moon conditions with focal trees offering 15 acorns of large, medium and  
214 small sizes (5 each). Acorn size is sampled from empirical distributions of these size  
215 categories. In each focal tree, the number of foraging events is drawn from a Poisson  
216 distribution with mean equal to the average number of events observed in the  
217 corresponding moon phase ( $\overline{\lambda_m}$ ). During each foraging event, simulated mice decide  
218 which acorn to handle and whether to remove it or not. If removed, mice decide to  
219 predate it or not after mobilization and acorn availability in the cage is updated. Once all

220 foraging events (of all trees) are simulated, acorn dispersal is modelled under full moon  
221 conditions (Supplementary File 3, Fig. S1).  
222 For each model run we sampled parameter of behavioral submodels (selection, removal  
223 and deposition) from posterior distributions fitted to data ( $\hat{\phi}_s$ , being  $s$  each behavioral  
224 submodel and  $\Phi$  its parameter set). Thus, in our simulations, mice adapted their  
225 decisions to acorn size and availability (in the experimental cage), characteristics of the  
226 focal tree (i.e. ungulate and predator scent presence), and the moon phase in which the  
227 foraging event occurs (new or full moon). After each model run (dispersal under new  
228 and full moon conditions), the program tracked the size and status of handled acorns  
229 and the environmental covariates in which the foraging event occurred. We run the  
230 model 1000 times and plotted deposition rates of viable acorns and their size with  
231 respect to the moon phase and tree characteristics (predator scent and ungulate  
232 presence). See Supplementary File 3 for detailed model specifications and Fig. S1 for a  
233 summary of the process overview.

234

## 235 **Results**

236 Before setting the cafeteria experiments in November, we removed from cages 53.3  
237 acorns/m<sup>2</sup> on average (range: 0-104). No acorn was found in February. We monitored  
238 2280 acorns under 38 focal trees. We detected mouse activity in 18 and 26 trees in the  
239 new and full moon of November, and in 26 and 24 trees in the new and full moon of  
240 February, respectively. Mice manipulated 1378 acorns. Out of them, 505 were  
241 mobilized outside cages and 385 (76%) were relocated [26].

242

### 243 **Foraging decisions in the focal tree: selection and removal**

244 In general, mice selected larger acorns, but the positive effect of size was modulated by  
245 environmental conditions. Size-driven selection preferentially occurred in the absence  
246 of competition with ungulates (Fig. 1A) and predator scent (Fig. 1B). In addition, mouse  
247 selectivity was enhanced under low local acorn availability (Table 1, selection). Among  
248 selected acorns, mice preferentially removed smaller ones. Such selective behavior  
249 occurred when risks were low due to reduced night brightness (new moon, Fig. 1C) or  
250 lack of predator scent (Fig. 1D), as well as when ungulates were absent (Table 2). Acorn  
251 availability at local and landscape scales did not modify size effects, although they  
252 changed mobilization rates. Rates were higher in lean periods (13% in November vs 24  
253 % in February) and when local availability was high (Table 2, removal).

254

#### 255 **Foraging decisions during dispersal: mobilization distances and predation**

256 Mice mobilized acorns closer under new moon conditions (Fig. 2A) and when ungulates  
257 were present (Fig. 2B). Even though acorn size did not affect overall mobilization  
258 distances, in February mice tended to mobilize smaller acorns further away (Table 2,  
259 Mobilization distances: Size\*Month). Regarding initial fates, post-dispersal predation  
260 increased during lean periods (February) and was relaxed in the presence of ungulates  
261 (Table 2, Viability after deposition). In addition, larger acorns were preferentially  
262 consumed (Fig. 2C), though the presence of ungulates attenuated this negative effect  
263 (Fig. 2D).

264

#### 265 **Transition probability model for acorn dispersal**

266 Under optimal conditions (new moon, no predator scent or ungulates), post-dispersal  
267 predation rates were higher (Fig. 3A) and simulated mice preferentially consumed large  
268 acorns (i.e. viable acorns were smaller, Fig. 3B-D, left bars). However, predation risks  
269 and ungulate presence precluded acorn consumption after mobilization and attenuated  
270 selection. As a result, the proportion of viable acorns increased and they were larger  
271 (Fig. 3A and B-D, right bars).

272

## 273 **Discussion**

274 Overall, our results show that environmental stress unbalances the oak-rodent  
275 interaction towards the mutualism side. When relaxed, mice preferentially consumed  
276 large acorns and removed small ones. Furthermore, mobilized seeds were more likely to  
277 be predated. In contrast, under stressful conditions (predation risk and competition)  
278 mice foraged opportunistically and reduced their activity outside tree canopies. As a  
279 result, predation rates after mobilization decreased, and larger acorns had a higher  
280 probability to survive. This bolsters the idea that interactions with third-party players  
281 can strongly affect seed dispersal effectiveness of scatter-hoarders [12, 15, 52]. Also,  
282 that intermediate stress can benefit plants by reducing the capacity of scatter-hoarders to  
283 recover mobilized seeds.

284 As expected, larger and more valuable acorns were preferentially handled by mice,  
285 which adapted this behavior to the environmental context [12]. In line with previous  
286 work, mice foraged opportunistically in trees with predator scent, probably because they  
287 devoted more time to vigilant behaviors [17, 27] at expenses of acorn discrimination  
288 [22]. In contrast, acorn availability effects did not follow the expectations of increased  
289 selectivity in scenarios of food depletion [28, 52, 53]. Seed size effects were similar

290 between acorn fall peaks and lean periods. Furthermore, mice foraged randomly when  
291 ungulates were present, while they selected larger seeds within exclosures. These  
292 unexpected results can be explained by some particularities of our system. Dehesas are  
293 characterized by high acorn production and scarce shrub cover (<1%) around trees [41,  
294 54, 55]. Under such circumstances, the effects of increased predation risks outside tree  
295 canopies can outweigh those of competition leading to a rapid and random harvesting of  
296 seeds [22]. In contrast, within ungulate exclosures, reduced grazing and soil compaction  
297 has promoted taller resprouts under canopies and increased cover of herbs and tussocks  
298 around trees [56]. As a result, in the absence of ungulates mice can forage under shelter  
299 and select the most profitable food items [17]. Taken together, these patterns point out  
300 that in dehesas, risk rather than competition modulates the effects of ungulate presence  
301 on acorn selection.

302 Larger acorns tend to be carried away, mobilized farther and preferentially cached in  
303 forests habitats [4, 26, 27, 34]. However, in our study larger acorns had a higher  
304 probability of being predated (*in situ* and after transportation) and seed size did not  
305 affect mobilization distances. Again, these results highlight that environmental  
306 conditions in dehesas are particularly harsh for rodents. In general, small seeds are  
307 preferentially mobilized when the costs of carrying large ones result unaffordable [12].  
308 In the presence of ungulates, low antipredatory cover and high trampling risks may have  
309 triggered transportation costs [13, 57], deterring mice from carrying large seeds away.  
310 Again, seed size effects were not fixed, but depended on direct and indirect cues of risk.  
311 Preferential removal of small seeds only occurred in trees with no predator scent or  
312 under new moon conditions, reflecting that only when risks are mild mice can take the  
313 time to select among the seeds available [15, 22].

314 Regarding post-dispersal survival, we expected higher predation when acorns were  
315 deposited close to tree canopies [13, 16]. Nonetheless, this relationship blurred in our  
316 system. Outside ungulate exclosures, larger acorns had a higher probability of escaping  
317 predation in spite of being mobilized nearby source trees. In dehesas, the pervasiveness  
318 of open land cover forces mice to concentrate their activities beneath canopies [13, 24,  
319 56], and decreases the likelihood that mobilized acorns are encountered and consumed  
320 [58]. Taken together, our results suggest that intermediate levels of stress can enhance  
321 seed dispersal effectiveness by mice (as suggested by [52, 59]). Accordingly, in our  
322 simulations, suboptimal conditions (due to increased risks or ungulate presence)  
323 enhanced dispersal. Increased risks discouraged mice from investing time in selecting  
324 which acorns to carry away and from consuming seeds after mobilization.  
325 Consequently, predation rates were reduced and larger acorns had a higher probability  
326 of dispersal. In Mediterranean systems, seedlings from larger acorns are more resistant  
327 to summer drought [29, 60], which represents the main recruitment bottleneck for oak  
328 regeneration [38, 61]. Thus, our simulation results suggest that suboptimal conditions  
329 can enhance both, the quantity and quality component of dispersal effectiveness by  
330 mice.

331 This work builds on previous research analyzing the effects of competition and risk on  
332 mouse foraging behavior in dehesas [17]. Here, by accounting for all stages of scatter-  
333 hoarding decisions (from initial manipulation to consumption after mobilization [4], and  
334 including the entire acorn fall season [27] as well as contrasting moon light conditions  
335 [22], we obtained a more in-depth understanding of the main drivers of dispersal  
336 effectiveness. Moreover, our transition probability model allowed us to assemble all  
337 stages of the scatter-hoarding process, and hence, to estimate the net effects of  
338 competition and risks on initial seed fate. However, future work that analyzes the actual

339 probability of recruitment of mobilized seeds is needed. In the Mediterranean area,  
340 seedling recruitment usually concentrates under the shade of shrubs, where conditions  
341 are milder [62-64]. Thus, it remains an open question whether higher rates of seedling  
342 dry out in dehesas (due to lack of shrub cover) can outweigh the benefits provided by  
343 enhanced cache survival. Once information about long-term survival of caches and  
344 seedling recruitment is available, it can be easily included in our model [65].

345

### 346 **Concluding remarks**

347 Our mechanistic approach provides new insights about the joint effect of habitat  
348 structure, competition and risk on dispersal effectiveness in synzoochorous interactions.  
349 In particular, we show that suboptimal conditions for scatter-hoarders can balance the  
350 interaction towards the mutualistic side. High predation risks forced mice to forage less  
351 efficiently resulting in a higher probability of post-dispersal survival of large acorns.  
352 Our work points out that environmental stress can be an important factor modulating the  
353 spatial and temporal dynamism of synzoochorous interactions [5]. Also, it supports the  
354 view that biological integrity (presence of the full set of producers, consumers,  
355 dispersers and predators) is key for ensuring seed dispersal effectiveness in  
356 synzoochorous conditional mutualisms [5, 52]. This may be particularly important in  
357 man-made habitats like dehesas, which depend on conditional mutualisms to ensure  
358 their long-term sustainability [38, 55].

359

### 360 **Supporting information**

#### 361 **S1. Structure of models and priors**

362 **S2. Posterior predictive checks**

363 **S3. Specifications of transition probability model for acorn dispersal**

364 **S4. Code for the transition probability model**

365 **S5. Databases**

366

367 **Acknowledgements**

368 D. López, M. Fernández and C. L. Alonso helped during fieldwork. D. López, B.  
369 Ramos and M. de Pablo pre-processed the video recordings, and D. Gallego, D. Valero,  
370 A. Velasco, C. J. González and E. Sánchez visualized the recordings noting seed  
371 choices. Authorities of the Cabañeros National Park provided the official permissions to  
372 carry out field experiments. J. España provided common genet scats. This study is a  
373 contribution to the projects RISKDISP (CGL2009-08430) and VULGLO (CGL2010-  
374 22180-C03-03), funded by the Spanish Ministry of Economy, and REMEDINAL3-CM  
375 (S2013/MAE-2719), funded by the Autonomous Community of Madrid. We declare no  
376 conflict of interest.

377

378 **Author contributions**

379 MD conceived and executed the field experiment with the aid of IT, IB, TM-L and AN-  
380 C. JS-D compiled the data and performed preliminary analyses and drafts. TM-L  
381 executed the final data analyses and proposed the final main focus of the paper. TM-L  
382 and MD wrote the final version of the paper on former versions drafted by JS-D and  
383 contributed by all authors.



384

385 **References**

- 386 1. Vander Wall SB. The evolutionary ecology of nut dispersal. *Bot Rev.* 2001;67: 74-117.  
387 ecosystems. *Funct Ecol.* 2020;34: 182-193.
- 388 2. den Ouden J, Jansen PA, Smit R. Jays, Mice and Oaks: Predation and Dispersal of *Quercus*  
389 *robur* and *Quercus petraea* in North-western Europe. In: Forget PM, Lambert JE, Hulme PE,  
390 editors. Seed Fate: Predation, dispersal, and seedling establishment. Wallingford: CAB  
391 International; 2005. pp. 223-239.
- 392 3. Pérez-Ramos IM, Urbietta IR, Marañón T, Zavala MA, Kobe RK 2008. Seed removal in two  
393 coexisting oak species: ecological consequences of seed size, plant cover and seed drop timing.  
394 *Oikos* 117,1386–1396.
- 395 4. Wang B, Ye CX, Cannon CH, Chen J. Dissecting the decision making process of  
396 scatter-hoarding rodents. *Oikos.* 2013;122: 1027-1034.
- 397 5. Gómez JM, Schupp EW, Jordano P. Synzoochory: the ecological and evolutionary relevance  
398 of a dual interaction. *Biol Rev.* 2019; 94: 874-902.
- 399 6. Theimer TC. Rodent scatterhoarders as conditional mutualists. In: Forget PM, Lambert JE,  
400 Hulme PE, editors. Seed Fate: Predation, dispersal, and seedling establishment. Wallingford:  
401 CAB International; 2005. pp. 283-295.
- 402 7. Bronstein JL. Conditional outcomes in mutualistic interactions. *Trends Ecol Evol.* 1994;9:  
403 214-217.
- 404 8. Sawaya GM, Goldberg AS, Steele MA, Dalglish HJ. Environmental variation shifts the  
405 relationship between trees and scatterhoarders along the continuum from mutualism to  
406 antagonism. *Integr Zool.* 2018;13: 319 – 330.
- 407 9. Pesendorfer M, Sillett ST, Koenig W Morrison S. Scatter-hoarding corvids as seed dispersers  
408 for oaks and pines: A review of a widely distributed mutualism and its utility to habitat  
409 restoration. *Condor.* 2016;118: 215-237.

- 410 **10.** Morán-López T, Alonso CL, Díaz M. Landscape effects on jay foraging behavior decrease  
411 acorn dispersal services in dehesas. *Acta Oecol.* 2015;69: 52–64.
- 412 **11.** Steele MA, Contreras TA, Hadj-Chikh, LZ, Agosta SJ, Smallwood PD, Tomlinson, CN. Do  
413 scatter hoarders trade off increased predation risks for lower rates of cache pilferage? *Behav*  
414 *Ecol.* 2014;25: 1–10.
- 415 **12.** Lichti NI, Steele MA, Swihart RK. Seed fate and decision-making processes in scatter-  
416 hoarding rodents. *Biol Rev.* 2017;92: 474–504.
- 417 **13.** Morán-López T, Wiegand T, Morales JM, Valladares F, Díaz M. Predicting forest  
418 management effects on oak–rodent mutualisms. *Oikos.* 2016;125: 1445-1457.
- 419 **14.** Puerta-Piñero C, Gómez JM, Schupp EW. Spatial patterns of acorn dispersal by rodents: do  
420 acorn crop size and ungulate presence matter? *Oikos.* 2010;119: 179-187.
- 421 **15.** Sunyer P, Muñoz A, Bonal R, Espelta JM. The ecology of seed dispersal by small rodents: a  
422 role for predator and conspecific scents. *Funct Ecol.* 2013;27: 1313–1321.
- 423 **16.** Morán-López T, Fernández M, Alonso CL, Flores D, Valladares F, Díaz M. Effects of forest  
424 fragmentation on the oak-rodent mutualism. *Oikos* 2015;124: 1482–1491.
- 425 **17.** Gallego D, Morán-López T, Torre I, Navarro-Castilla A, Barja I, Díaz M. Context  
426 dependence of acorn handling by the Algerian mouse (*Mus spretus*). *Acta Oecol.* 2017; 84: 1-7.
- 427 **19.** Díaz M. Rodent seed predation in cereal crop areas of central Spain—Effects of  
428 physiognomy, food availability, and predation risk. *Ecography.* 1992;15: 77–85
- 429 **20.** Orrock, JL, Danielson BJ, Brinkerhoff R. Rodent foraging is affected by indirect, but not by  
430 direct, cues of predation risk. *Behav Ecol.* 2004;15: 433–437.
- 431 **21.** Díaz M, Torre I, Peris A, Tena L. Foraging behaviour of wood mice as related to the  
432 presence and activity of genets. *J Mammal* 2005;86: 1178-1185.
- 433 **22.** Perea R, González R, San Miguel A, Gil L. Moonlight and shelter cause differential seed  
434 selection and removal by rodents. *Anim Behav.* 2011;82: 717–723.
- 435 **23.** Navarro-Castilla A, Barja, I. Antipredatory response and food intake in woodmice  
436 (*Apodemus sylvaticus*) under simulated predation risk by resident and novel carnivorous  
437 predators. *Ethol.* 2014;120: 90–98.

- 438 **24.** Navarro-Castilla A, Barja I, Díaz M. Foraging, feeding, and physiological stress responses  
439 of wild wood mice to increased illumination and common genet cues. *Current Zool.* 2018;64:  
440 409–417.
- 441 **25.** Pons J, Pausas JG. Rodent acorn selection in a Mediterranean oak landscape. *Ecol Res.*  
442 2007;22: 535–541.
- 443 **26.** Gómez JM, Puerta-Piñero C, Schupp EW. Effectiveness of rodents as local seed dispersers  
444 of Holm oaks. *Oecologia.* 2008;155: 529-537.
- 445 **27.** Muñoz A, Bonal R. Are you strong enough to carry that seed? Seed size/body size ratios  
446 influence seed choices by rodents. *Anim Behav.* 2008;76: 709–715.
- 447 **27.** Sunyer P, Espelta JM, Bonal R, Muñoz A. Seeding phenology influences wood mouse seed  
448 choices: the overlooked role of timing in the foraging decisions by seed-dispersing rodents.  
449 *Beha Ecol Sociobiol.* 2014;68: 1205–1213.
- 450 **28.** Morán-López T, Valladares F, Tiribelli F, Pérez-Sepúlveda JE, Traveset A, Díaz M.  
451 Fragmentation modifies seed trait effects on scatter-hoarders’ foraging decisions. *Plant Ecol.*  
452 2018;219: 325–342.
- 453 **29.** Gómez JM. Bigger is not always better: conflicting selective pressures on seed size in  
454 *Quercus ilex*. *Evolution.* 2004;58: 71-80.
- 455 **30.** Schupp E, Jordano P, Gómez JM. Seed dispersal effectiveness revisited: a conceptual  
456 review. *New Phytol.* 2010;188: 333-353.
- 457 **31.** Zwolak R, Crone EE. Quantifying the outcome of plant – granivore interactions. *Oikos.*  
458 2012;121: 20–27.
- 459 **32.** Vander Wall SB. Masting in animal-dispersed pines facilitates seed dispersal. *Ecology.*  
460 2002;83: 3508–3516.
- 461 **33.** Li HJ, Zhang ZB. Effects of mast seeding and rodent abundance on seed predation and  
462 dispersal by rodents in *Prunus armeniaca* (Rosaceae). *Forest Ecol Manage.* 2007;242: 511-517.
- 463 **34.** Wang J, Zhang B, Hou X, Chen X, Han N, Chang G. Effects of mast seeding and rodent  
464 abundance on seed predation and dispersal of *Quercus aliena* (Fagaceae) in Qinling Mountains,  
465 Central China. *Plant Ecol.* 2017;218: 1–11.

- 466 **35.** Pulliam HR. Foraging efficiency, resource partitioning, and the coexistence of sparrow  
467 species. *Ecology*. 1985;66: 1829-1836.
- 468 **36.** Díaz M. Variability in seed size selection by granivorous passerines. Effects of bird size,  
469 bird size variability, and ecological plasticity. *Oecologia*. 1994;99: 1-6
- 470 **37.** Campos P, Huntsinger L, Oviedo JL, Díaz M, Starrs P, Standiford RB, Montero G, editors.  
471 Mediterranean Oak Woodland Working Landscapes: Dehesas of Spain and Ranchlands of  
472 California. New York: Springer; 2013.
- 473 **38.** Díaz M, Sánchez-Mejía T, Morán-Lopez T. Long-term tree regeneration of fragmented  
474 agroforestry systems under varying climatic conditions. *Frontiers Ecol Evol*. 2021;9: 96.
- 475 **39.** Díaz M, González E, Muñoz-Pulido R, Naveso MA. Effects of food abundance and habitat  
476 structure on seed-eating rodents wintering in Spanish man-made habitats. *Z Säugetier*. 1993;58:  
477 302-311.
- 478 **40.** Muñoz A, Bonal R, Díaz M. Ungulates, rodents, shrubs: interactions in a diverse  
479 Mediterranean ecosystem. *Basic Appl Ecol*. 2009;10: 151-160.
- 480 **41.** Pulido FJ, Díaz M, Hidalgo S. Size structure and regeneration of Spanish holm oak *Quercus*  
481 *ilex* forests and dehesas: effects of agroforestry use on their long-term sustainability. *Forest Ecol*  
482 *Manage*. 2001;146: 1–13.
- 483 **42.** Jiménez J. El ciervo (*Cervus elaphus*) en la zona oriental del Parque Nacional de Cabañeros.  
484 Madrid: Organismo Autónomo Parques Nacionales; 2004.
- 485 **43.** Perea R, Gil L. Tree regeneration under high levels of wild ungulates: The use of chemically  
486 vs. physically-defended shrubs. *Forest Ecol Manage*. 2014;312: 47-54.
- 487 **44.** Pulido F, García E, Obrador JJ, Moreno G. Multiple pathways for tree regeneration in  
488 anthropogenic savannas: incorporating biotic and abiotic drivers into management schemes. *J*  
489 *Appl Ecol*. 2010;47: 1272-1281.
- 490 **45.** Díaz M, Alonso CL, Beamonte E, Fernández M, Smit C. Development of a long-term  
491 monitoring protocol of keystone organisms for the functioning of Mediterranean forests [in  
492 Spanish]. In: Ramírez L, Asensio B, editors. *Proyectos de investigación en parques nacionales:*  
493 *2007-2010*. Madrid, Organismo Autónomo Parques Nacionales. 2011. pp. 47–75.

- 494 **46.** Palomo LJ, Justo ER, Vargas JM. *Mus spretus* (Rodentia: Muridae). Mamm Spec.  
495 2009;840: 1–10.
- 496 **47.** Torre I, Arrizabalaga A, Freixas L, Ribas A, Flaquer C, Díaz M. Using scats of a generalist  
497 carnivore as a tool to monitor small mammal communities in Mediterranean habitats. Basic  
498 Appl Ecol. 2013;14: 155–164.
- 499 **48.** Torre I, Raspall A, Arrizabalaga A, Díaz M. SEMICE: An unbiased and powerful  
500 monitoring protocol for small mammals in the Mediterranean Region. Mamm. Biol. 2018;88:  
501 161–167.
- 502 **49.** Sikes RS, Gannon WL. Guidelines of the American Society of Mammalogists for the use of  
503 wild mammals in research. J Mammal. 2011;92: 235-253.
- 504 **50.** Wenny DG. Effects of human handling of seeds on seed removal by rodents. Am Midl Nat.  
505 2002;147: 404–408.
- 506 **51.** Plummer M. JAGS: A program for analysis of Bayesian graphical models using Gibbs  
507 sampling. Proceedings of the 3rd International workshop on distributed statistical computing;  
508 2003.
- 509 **52.** Schupp EW, Zwolak R, Jones LR, Snell RS, Beckman NG, Aslan C, Cavazos BR, Effiom  
510 E, Fricke EC, Montaña-Centellas F, Poulsen J, Razafindratsima OH, Sandor ME, Shea K.  
511 Intrinsic and extrinsic drivers of intraspecific variation in seed dispersal are diverse and  
512 pervasive. AoB Plants. 2019;11: plz067.
- 513 **53.** Stephens DW, Krebs JR. Foraging theory. Princeton: Princeton University Press; 1986.
- 514 **54.** Koenig WD, Díaz M, Pulido F, Alejano R, Beamonte E, Knops JMH. Acorn production  
515 patterns. In Campos P, Huntsinger L, Oviedo JL, Díaz M, Starrs P, Standiford RB, Montero G,  
516 editors. Mediterranean Oak Woodland Working Landscapes: Dehesas of Spain and Ranchlands  
517 of California. New York: Springer; 2013. pp. 181-209.
- 518 **55.** Díaz M. Tree scattering and long-term persistence of dehesas: patterns and processes [in  
519 Spanish]. Ecosistemas. 2014;23: 5-12.

- 520 **56.** Navarro-Castilla A, Díaz M, Barja I. Does ungulate disturbance mediate behavioural and  
521 physiological stress responses in Algerian mice *Mus spretus*? A wild enclosure experiment.  
522 *Hystrix*. 2017;28: 165–172.
- 523 **57.** Muñoz A, Bonal R. Rodents change acorn dispersal behaviour in response to ungulate  
524 presence. *Oikos*. 2007;116: 1631-1638.
- 525 **58.** Muñoz A, Bonal R. Linking seed dispersal to cache protection strategies. *J Ecol*. 2011;99:  
526 1016-1025.
- 527 **59.** Feldman M, Ferrandiz-Rovira M, Espelta JM, Muñoz A. Evidence of high individual  
528 variability in seed management by scatter-hoarding rodents: does “personality” matter? *Anim*  
529 *Behav*. 2019;150: 167-174.
- 530 **60.** Bonito A, Varone L, Gratani L. Relationship between acorn size and seedling morphological  
531 and physiological traits of *Quercus ilex* L. from different climates. *Photosynthetica*. 2011;49:  
532 75–86.
- 533 **61.** Pulido FJ, Díaz M. Regeneration of a Mediterranean oak: a whole-cycle approach.  
534 *EcoScience*. 2005;12: 92-102.
- 535 **62.** Ramírez JA, Díaz, M. The role of temporal shrub encroachment for the maintenance of  
536 Spanish holm oak *Quercus ilex* dehesas. *Forest Ecol Manage*. 2008;255: 1976–1983.
- 537 **63.** Smit C, den Ouden J, Díaz M. Facilitation of *Quercus ilex* recruitment by shrubs in  
538 Mediterranean open woodlands. *J Veget Sci*. 2008;19: 193-200.
- 539 **64.** Smit C, Díaz M, Jansen P. Establishment limitation of holm oak (*Quercus ilex* subsp.  
540 *ballota* (Desf.) Samp.) in a Mediterranean savanna–forest ecosystem. *Ann For Sci*. 2009;66: 1-  
541 7.
- 542 **65.** Morán-López T, González-Castro A, Morales JM, Nogales M. Behavioural  
543 complementarity among frugivorous birds and lizards can promote plant diversity in island  
544

**Table 1.** Summary table of the effects of size, moonlight, month, ungulate presence, predator scent and local acorn availability (and their interactions with size) on the probability of acorn selection and removal.

Process	Fixed effect	Mean	HPD1	f	
Acorn selection	<b>Size</b>	<b>0.19</b>	<b>[0.09, 0.29]</b>	<b>1.00</b>	**
	Moon (Full)	0.03	[-6.22, 6.35]	0.50	
	Month (February)	-0.03	[-6.12, 6.06]	0.50	
	Ungulate (Yes)	-0.05	[-6.27, 6.16]	0.51	
	Scent (Yes)	0.01	[-6.16, 6.28]	0.50	
	Availability	-0.02	[-6.32, 6.19]	0.50	
	Size*Moon	0.07	[-0.03, 0.17]	0.93	
	Size*Month	-0.06	[-0.16, 0.04]	0.88	
	<b>Size*Ungulates</b>	<b>-0.13</b>	<b>[-0.23, -0.03]</b>	<b>0.99</b>	**
	<b>Size*Scent</b>	<b>-0.08</b>	<b>[-0.18, 0.01]</b>	<b>0.96</b>	*
	<b>Size*Availabilitiy</b>	<b>-0.04</b>	<b>[-0.09, 0.01]</b>	<b>0.95</b>	*
	Acorn removal	<b>Size</b>	<b>-0.50</b>	<b>[-0.94, -0.07]</b>	<b>0.99</b>
Moon (Full)		0.07	[-0.27, 0.39]	0.65	
<b>Month (February)</b>		<b>0.77</b>	<b>[0.43, 1.11]</b>	<b>1.00</b>	**
Ungulate (Yes)		-0.22	[-0.96, 0.47]	0.73	
Scent (Yes)		0.20	[-0.53, 0.93]	0.72	
<b>Availability</b>		<b>0.29</b>	<b>[0.12, 0.46]</b>	<b>1.00</b>	**
<b>Size*Moon</b>		<b>0.29</b>	<b>[-0.02, 0.60]</b>	<b>0.96</b>	*
Size*Month		-0.09	[-0.41, 0.22]	0.71	
<b>Size*Ungulates</b>		<b>0.24</b>	<b>[-0.07, 0.55]</b>	<b>0.94</b>	•
<b>Size*Scent</b>		<b>0.30</b>	<b>[0.00, 0.59]</b>	<b>0.98</b>	*
Size*Availabilitiy	0.10	[-0.07, 0.26]	0.88		

546

547 Mean of posterior distribution, highest posterior density interval (HPD) and percentage of the posterior

548 distribution with the same sign as the mean (f) are shown. Effects with  $f \geq 0.95$  are in bold. • depicts  $f \in$

549 [0.90, 0.95)

551

**Table 2.** Summary table of the effects of size, moonlight, month, ungulate presence, predator scent and local acorn availability (and their interactions with size) on acorn mobilization distances and the probability that it is deposited in a viable status (vs predated).

Process	Fixed effect	Mean	HPD	f	
Mobilization distance	Size	0.52	[-0.35, 1.38]	0.88	
	<b>Moon (Full)</b>	<b>-0.78</b>	<b>[-1.49, -0.09]</b>	<b>0.99</b>	*
	Month (February)	0.16	[-0.61, 0.91]	0.66	
	<b>Ungulate (Yes)</b>	<b>-0.86</b>	<b>[-1.83, 0.18]</b>	<b>0.95</b>	*
	Scent (Yes)	-0.01	[-0.99, 1.07]	0.52	
	Availability	0.07	[-0.27, 0.42]	0.66	
	Size*Moon	-0.19	[-0.84, 0.46]	0.72	
	<b>Size*Month</b>	<b>-0.47</b>	<b>[-1.17, 0.22]</b>	<b>0.91</b>	•
	Size*Ungulates	-0.02	[-0.69, 0.65]	0.53	
	Size*Scent	0.13	[-0.52, 0.78]	0.65	
Size*Availabilitiy	-0.15	[-0.54, 0.22]	0.79		
Viability after deposition	<b>Size</b>	<b>-1.06</b>	<b>[-2.2, 0.03]</b>	<b>0.97</b>	*
	Moon (Full)	0.37	[-0.53, 1.26]	0.80	
	<b>Month (February)</b>	<b>-1.73</b>	<b>[-2.73, -0.77]</b>	<b>1.00</b>	*
	<b>Ungulate (Yes)</b>	<b>0.90</b>	<b>[-0.15, 2.04]</b>	<b>0.95</b>	*
	Scent (Yes)	-0.26	[-1.35, 0.8]	0.69	
	<b>Availability</b>	<b>0.37</b>	<b>[-0.12, 0.89]</b>	<b>0.93</b>	•
	Size*Moon	0.42	[-0.46, 1.33]	0.82	
	Size*Month	0.28	[-0.65, 1.21]	0.72	
	<b>Size*Ungulates</b>	<b>0.66</b>	<b>[-0.25, 1.63]</b>	<b>0.92</b>	•
	Size*Scent	0.27	[-0.6, 1.14]	0.73	
Size*Availabilitiy	-0.11	[-0.69, 0.46]	0.65		

552 Mean of posterior distribution, highest posterior density interval (HPD) and percentage of the posterior

553 distribution with the same sign as the mean (f) are shown. Effects with  $f \geq 0.95$  are in bold. • depicts  $f \in$

554 [0.90, 0.95)



556 **Figure legends**

557

558 **Fig. 1.** Mouse foraging decisions during acorn selection and removal (upper and  
559 lower panels, respectively). Mouse preferentially selected larger acorns. However, such  
560 selective behavior only occurred when (A) ungulates were absent and (B) there was no  
561 predator scent. Among selected acorns, mouse tended to mobilize smaller ones. This  
562 selective behavior occurred when risks were low due to (C) new moon conditions or (D)  
563 lack or predator scent. Also, when ungulates were absent (Table 1). Points represent  
564 mean values, bars standard errors.

565

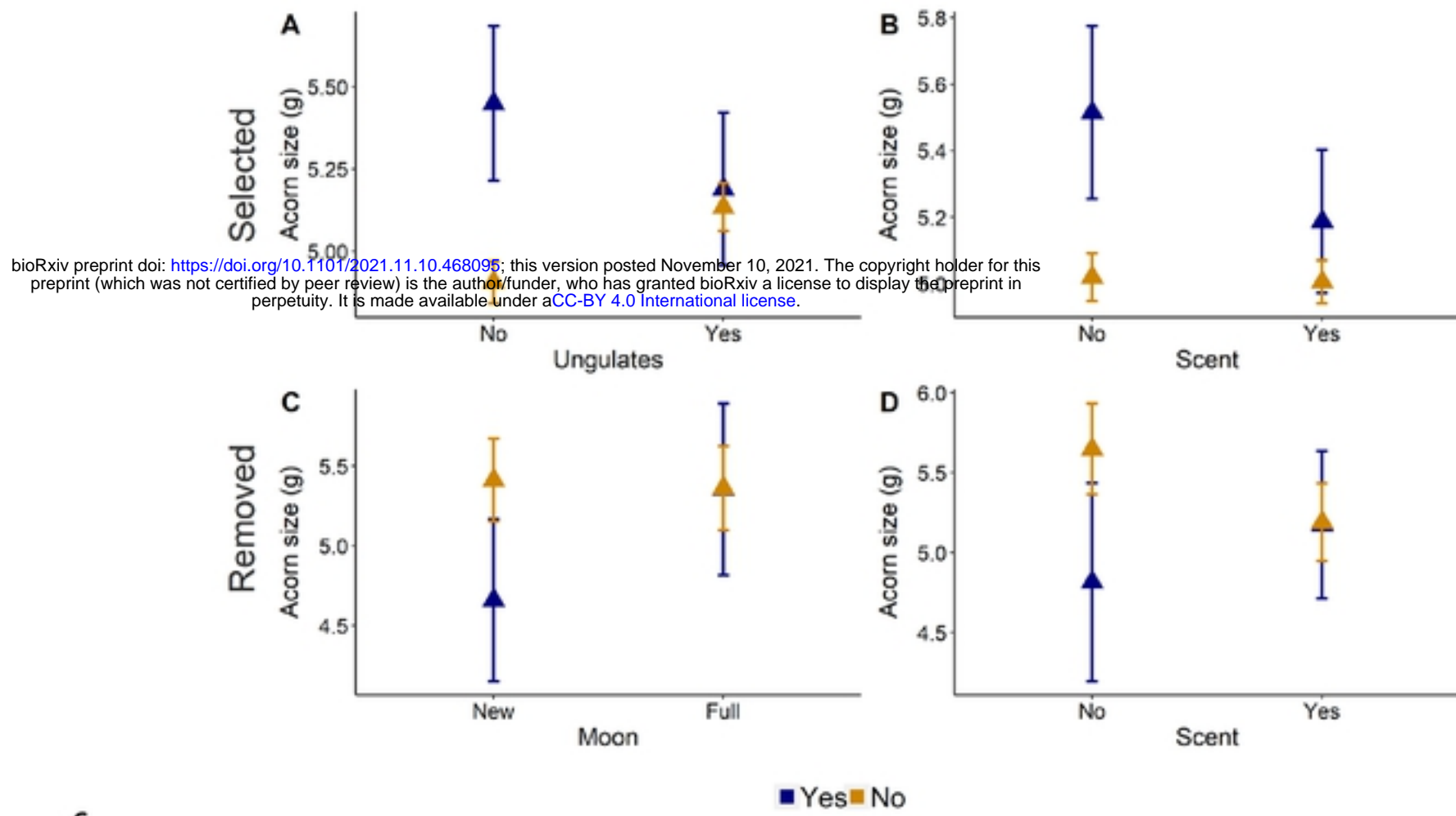
566 **Fig. 2.** Summary of mouse foraging decisions during and after mobilization. (A)  
567 Under full moon conditions and (B) in the presence of ungulates mice mobilized acorns  
568 closer. Regarding deposition, (C) larger acorns had a lower probability of escaping  
569 predation as well as (B) those mobilized in areas with ungulates. Black line in panel C  
570 represents mean effects of acorn size on the probability of escaping predation, and  
571 shaded area 0.95 credible intervals. Panel D, represents the proportion of viable acorns  
572 (after deposition) from trees inside and outside ungulate exclosures.

573

574 **Fig. 3.** Results from simulations of the probability transition model for acorn  
575 dispersal. (A) Under more stressful conditions (black bars), the proportion of acorns  
576 escaping predation increased. In general, mice tended to predate larger acorns under (B)  
577 new moon conditions, (C) in the presence of predator scent and (D) when competing  
578 with ungulates. Under more stressful conditions (Fig. B-D, right bars), mice were less  
579 selective and consequently size effects on acorn predation were attenuated (B),  
580 disappeared (C) or reversed (D). Bars represent mean values ( $\pm$ s.e.) across 1000  
581 simulations.

1  
2  
3  
4  
5

**Fig. 1**



6

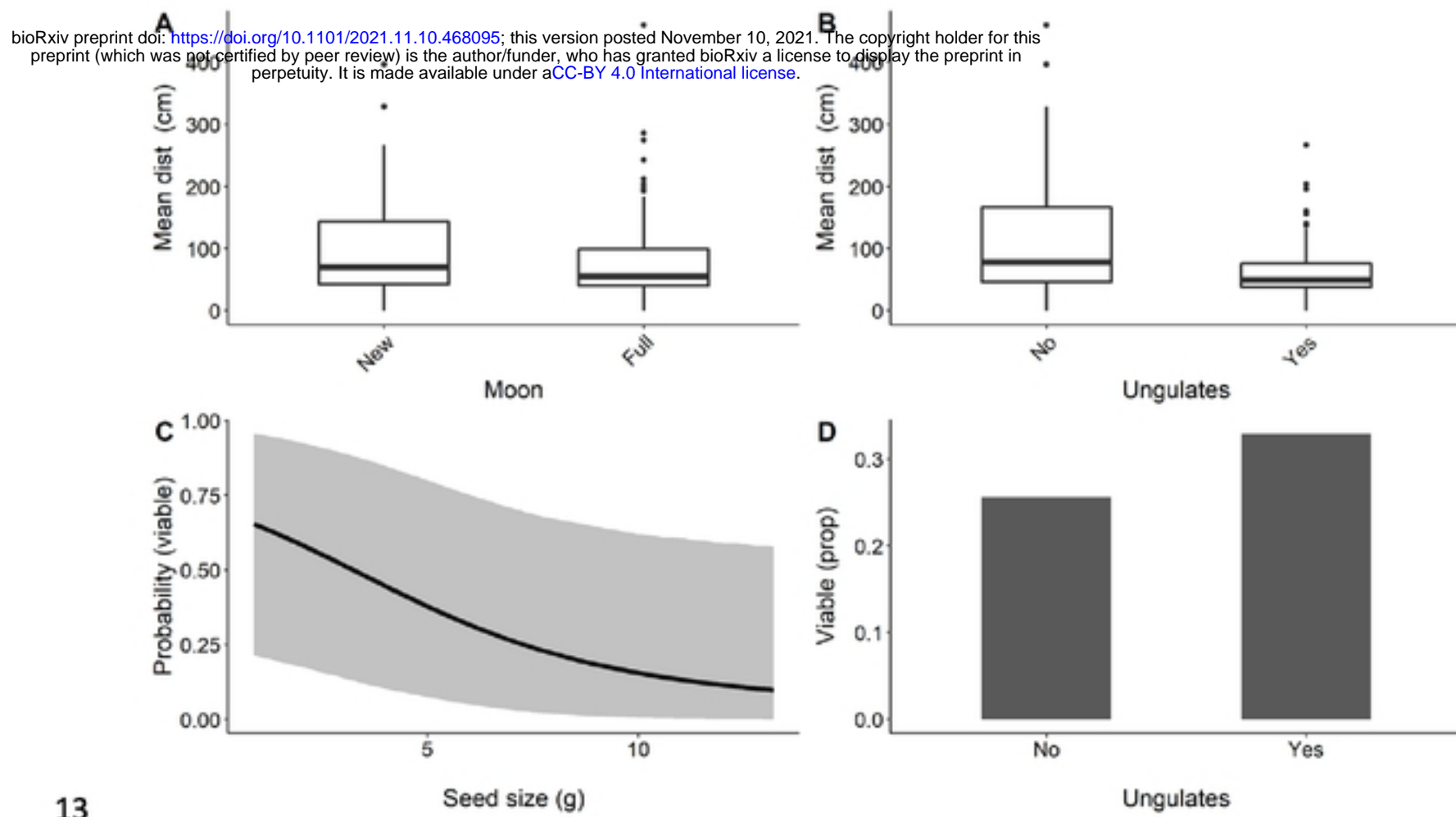
8

9 **Fig. 2**

10

11

12



13

14

15

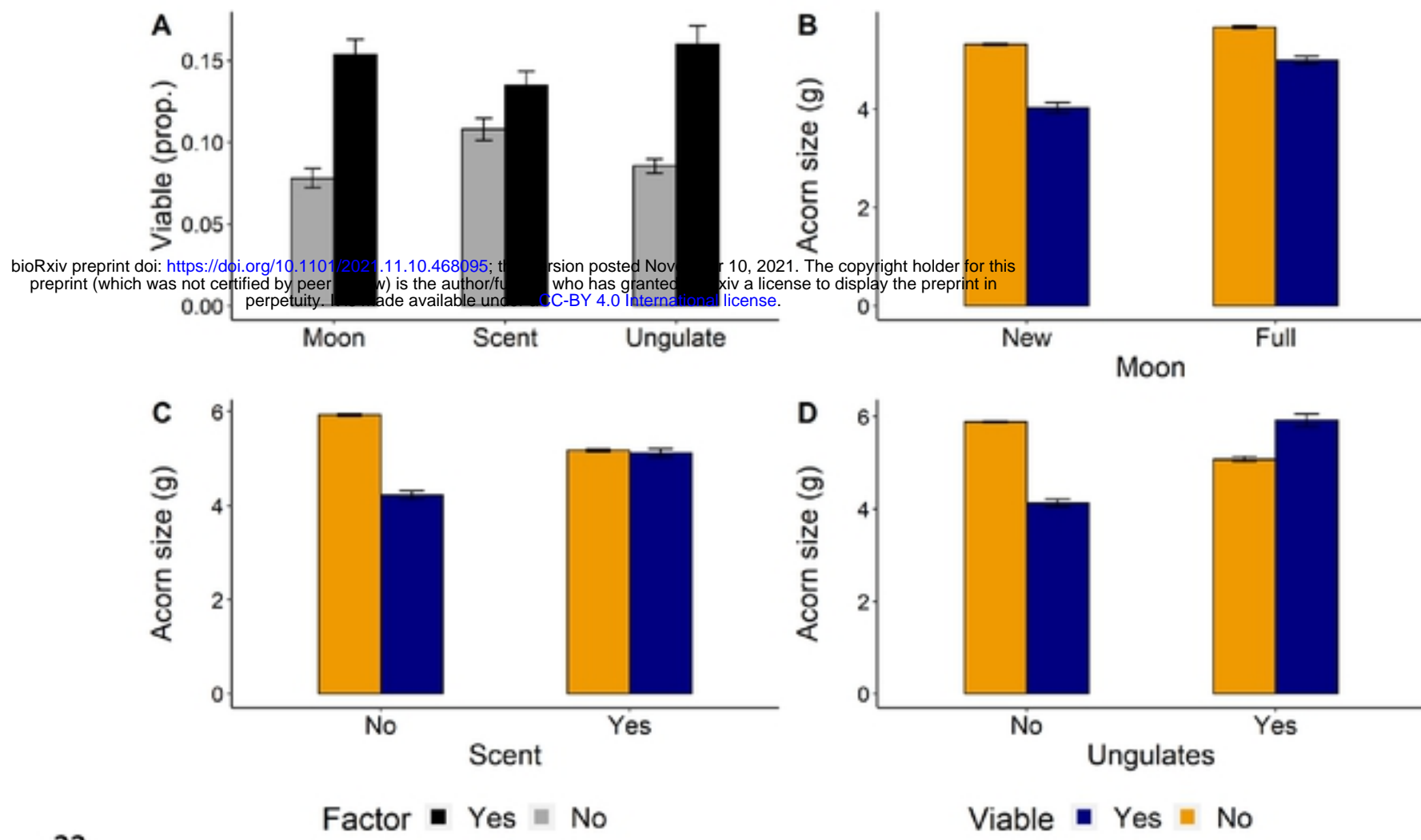
16

17

19 **Fig. 3**

20

21



22

23

24