

1 Original research article

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3 **Effect of patch size on seed removal by harvester ants**

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17 **Running head:** effect of Patch size on seed removal by ants

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26 **Summary**

27 **229 words**

28 The harvester ant *Messor barbarus* can be responsible for high weed seed losses in  
29 dryland cereals in Spain. Because weeds occur in patches, harvester ants have to be able  
30 to find and exploit patches. However, seed patches can differ in size and may, therefore,  
31 differ in the probability of being discovered and exploited. Here, 90 patches varying in  
32 size from 0.25 to 9 m<sup>2</sup> were created in three 50 x 50 m subareas in a cereal field. Oat  
33 seeds were sown, as weed seed surrogates, in the patches at 2000 seeds m<sup>-2</sup>. After 24 h,  
34 those remaining were collected and the exploitation rate (the percentage of seeds  
35 removed per patch discovered by ants) was estimated. Harvester ant nests and the  
36 location of the seed patches were georeferenced and used to estimate distances between  
37 them. The patch encounter rate (the proportion of patches discovered by the ants)  
38 decreased slightly, but significantly, with decreasing patch size, though not the  
39 exploitation rate, which was lowest in the smallest patches (78-94%) and highest in the  
40 largest (99-100%). Seed patches that were not found or partially exploited were mostly  
41 located in subareas with a lower ant nest density or a longer distance away from the  
42 nearest nest than seed patches that were fully exploited. The results of this study indicate  
43 that the interaction between the spatial distribution of ant nests and the patchy  
44 distribution of seeds can create opportunities for seeds to be subjected to lower levels of  
45 predation.

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47 **Keywords:** patch encounter, patch exploitation, *Messor barbarus*, seed predation, spatial  
48 distribution, dryland cereals

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59 **Introduction**

60

61 Harvester ants (genus *Messor*) are the most abundant granivores in rain-fed arable fields  
62 in NE Spain. Depending on the weed species, *Messor barbarus* (L.) can take 46-100% of  
63 all newly produced weed seeds, thus contributing to weed control (Westerman *et al.*,  
64 2012). Seed predation risk can vary considerably among and within dryland cereal fields  
65 (Díaz, 1992; Azcárate & Peco, 2003; Baraibar *et al.*, 2009; 2011c). Understanding this  
66 variability may be important in order to find ways to maximize weed seed losses.

67

68 Weeds tend to have a patchy spatial distribution, with some areas that are densely  
69 populated and other areas that are void of weeds (e.g., Johnson *et al.*, 1996). The  
70 magnitude of seed predation depends, in part, on the ability of granivores to locate  
71 spatially variable resources (Daedlow *et al.*, 2014). Variability in weed abundance across  
72 a field could be one of the factors responsible for the observed spatial variability in seed  
73 removal rate. Seed patch ‘quality’, defined in terms of patch size, resource density or  
74 resource composition (i.e. Brown *et al.*, 1988; Wellenreuther & Connell, 2000) could  
75 influence the foraging behaviour of seed predators and this, in turn, could be an important  
76 factor influencing patch and weed dynamics. For example, if harvester ants would focus  
77 their efforts preferably on ‘high quality’ patches, sustained high seed mortality over  
78 multiple years could eventually lead to the elimination of patches. In contrast, ‘low  
79 quality’ patches could experience low seed losses due to predation, resulting in  
80 population growth and patch expansion.

81

82 The dispersal ability and activity radius of the seed predators determine the scale  
83 at which differences in patch quality can be distinguished. For example, rodents can  
84 move hundreds of meters, allowing them to locate larger-sized patches, while  
85 invertebrates, such as beetles and crickets, move at a scale of a few dozen meters,  
86 limiting their ability to detect larger patches (e.g. Baraibar *et al.*, 2012; Marino *et al.*,  
87 2005; Heggenstaller *et al.*, 2006). Harvester ants forage at an intermediate scale of up to

88 30 meters (Azcárate & Peco, 2003). It is currently unknown how patch size influences  
89 seed patch selection and utilisation in the case of *M. barbarus* in arable fields.

90

91 In this study, we investigated whether patch size influences patch utilisation by  
92 harvester ants. We hypothesized that smaller patches would have a lower probability of  
93 being found than larger patches, forming an escape mechanism by which weeds may  
94 persist. Patch utilisation by seed predators can be divided into two sequential  
95 components, namely the probability of patch encounter and the rate of patch exploitation  
96 (Hulme, 1994). By creating seed patches of different size, but equal seed density per  
97 square meter, we tried to eliminate differences in the exploitation rate. However, we  
98 realize that because the total amount of seeds differed between patches (surface area ×  
99 seed density), this may be sufficient to trigger differences in the exploitation rate.

100

101 Seed predation is affected by the harvester ant behaviour and also by the spatial  
102 relationship of ant nests relative to the patch location. The probability of finding a  
103 resource decreases with the distance to the nest, as foraging intensity declines  
104 exponentially with distance from the nest (Azcárate & Peco, 2003). Díaz (1992) reported  
105 a 50% decrease in foraging efficiency at distances more than 1.5 m from the nest for  
106 *Messor capitatus* Latreille, a close relative of *M. barbarus*. *Messor barbarus* colonies  
107 tend to be regularly distributed at small spatial scales ( $\leq 4$  m), but can occur more  
108 clustered at larger scales (4-12 m), meaning that some parts of the field may contain more  
109 nests than other parts (Blanco-Moreno *et al.*, 2014). A clustered spatial distribution of  
110 harvester ant nests in combination with a clustered distribution of seed patches could  
111 explain the observed variability in seed predation (Azcárate & Peco, 2003; Baraibar *et*  
112 *al.*, 2011c). We hypothesized that the probability of patches being discovered would be  
113 lower in subareas with low densities of ant nests compared to more densely populated  
114 subareas.

115

## 116 **Materials and Methods**

117

118 A trial was conducted in a commercial, no-till cereal field, one month after crop harvest,  
119 in Villanova de Bellpuig (41° 35' 25.76" N, 0° 58' 36.28" E, sandy clay soil) in NE Spain  
120 in 2010. An experimental area (150 × 50 m) was divided into three subareas (A, B and C)  
121 of 50 × 50 m each, at least 20 m from the field margin. In each subarea, 38 square areas,  
122 called 'patches', were located randomly. Thirty patches per subarea were used to estimate  
123 seed removal by predators in response to patch size (exposed patches). Five patches  
124 (controls) were used to obtain information on the density of seeds naturally available on  
125 the soil surface before seed application. Three patches were used to test the efficiency of  
126 the machinery used to retrieve seeds (efficiency patches). Per subarea, the exposed  
127 patches were available in four different sizes; 16 patches of the smallest size (size 1; 0.25  
128 m<sup>2</sup>; 0.5 m × 0.5 m); eight patches of medium-small size (size 2; 1 m<sup>2</sup>; 1 m × 1 m); four  
129 patches of medium-large size (size 3; 3 m<sup>2</sup>; 1.73 m × 1.73 m) and two large patches (size  
130 4; 9 m<sup>2</sup>; 3 m × 3 m). The minimum distance between patches and between patch and edge  
131 of the subarea was 1 m. Patch areas were prepared by removing straw by raking and  
132 sweeping, outlining the area by carving the perimeter in the soil surface with a knife, and  
133 staking its corners with coloured stakes. Next, the areas were seeded with 2000 *Avena*  
134 *sativa* L. seeds m<sup>-2</sup> (Semillas Batlle, Bell-Lloc, Spain), as determined by weight, using a  
135 seed weight of 73 ± 0.4 g per 2000 seeds. To obtain a uniform weight, seeds were first  
136 dried in an oven at 40 °C for 4 hours. Seeds were applied on the surface by hand during  
137 the early morning hours (7:00 - 7:30 h). This was done while wearing gloves, such that  
138 ants would not be influenced by seeds that had been handled by humans. Oat seeds are a  
139 good substitute for weed seeds, because they are readily taken by harvester ants (Heredia  
140 & Detraint, 2005), because estimated removal rates (see Results section) are similar to  
141 those previously reported for weed seeds (Westerman *et al.*, 2012; Baraibar *et al.*, 2011a;  
142 2011c; Atanackovic, 2013), and because oat seeds could easily be distinguished from  
143 straw and soil, which facilitated seed recovery and counting. The experiment was  
144 initiated sequentially in time, namely on 10 August in subarea A, 16 August in B, and 17  
145 August in C. Twenty-four hours after seed application, seeds were retrieved using a D-  
146 Vac (Vortis; Burkard manufacturing Co. Ltd., Rickmansworth) operated for  
147 approximately two minutes per square meter. In the case of patches of sizes 1 and 2, the  
148 entire area was vacuum cleaned. In patches of size 3, two sub-areas of 1 m<sup>2</sup> were vacuum

149 cleaned; in patches of size 4, three sub-areas of 1 m<sup>2</sup> were vacuum cleaned. All material  
150 collected, i.e. seeds, soil and plant debris, was stored in a paper bag until further  
151 processing. Samples were dried, sieved, cleaned, and weighed to estimate the number of  
152 seeds retrieved.

153

154 To assess the density of seeds naturally available on the soil surface, five control  
155 patches (1 m<sup>2</sup>) in each subarea without seeding were sampled one day before seed  
156 application. Soil surface samples were collected in paper bags and processed as described  
157 above.

158

159 The efficiency of the D-vac at retrieving the applied seeds was determined in  
160 three randomly selected patches (1 m<sup>2</sup>) per subarea. Seeds were applied (2000 seeds m<sup>-2</sup>)  
161 on the soil surface one hour before seeding in the exposed patches, and retrieved  
162 immediately to avoid seed removal by ants. Soil surface samples were collected in paper  
163 bags and processed as described above. Seeds may become inaccessible, for example,  
164 when they fall into cracks and crevices such as found around the base of cereal stubble.

165

166 Ants are most active when the soil temperature is between 15 and 35 °C (Azcárate  
167 *et al.*, 2007). Therefore, average hourly air temperatures were monitored at a weather  
168 station located in Tornabous (46°17'40" N, 33°73'16" E), 10 km from the experimental  
169 site (Generalitat de Catalunya, 2012).

170

171 Ant nest density and spatial distribution was determined by counting and  
172 georeferencing all nests in each subarea, as described in Blanco-Moreno *et al.* (2014). In  
173 short, subareas were divided into 25, 10 m × 10 m areas to ease counting. Counting and  
174 georeferencing of all ant nests was done on 10 August, 16 August, and 17 August 2010  
175 between 7:00 (sunrise) and 12:00 h (noon), after which temperatures became prohibitive  
176 for ant activity (Azcárate *et al.*, 2007). Similarly, the location of seed patches and  
177 subareas were georeferenced, using a GPS with sub-metric precision (Trimble®  
178 GeoXHTM hand-held, GeoExplorer®, 2005).

179

180 *Data analysis*

181 *Sampling efficiency* The sampling efficiency,  $E$ , of the D-Vac was calculated as the ratio  
182 between the weight of the seeds recovered ( $S_r$ ) and the initial seed weight applied ( $S_i$ ):

183

$$184 \quad E = \left( \frac{S_r}{S_i} \right) \quad (1)$$

185

186 The average sampling efficiency across all efficiency patches and subareas ( $\bar{E}$ )  
187 was used as a correction factor in further calculations (see below). The lowest value  
188 found for the efficiency of the D-vac across patches and subareas,  $X$ , was used as a  
189 conservative estimate of  $Y$  ( $=1-X$ ), the threshold value beyond which patches were  
190 assumed to have been found and exploited by ants. Any patch for which the proportion of  
191 seeds lost was higher than  $Y$  was assumed to have been found and exploited by ants.

192

193 *Seed removal* The seed removal rate,  $R$ , defined as the percentage of seeds removed per  
194 patch discovered by ants, was estimated as the difference between initial ( $S_i$ ) and  
195 recovered seed weight ( $S_r$ ), corrected for  $\bar{E}$ , and relative to the initial seed weight,

196

$$197 \quad R = \frac{\left( S_i - \frac{S_r}{\bar{E}} \right)}{S_i} \cdot 100 \quad (2)$$

198

199 A linear mixed regression model (quasi-binomial distribution, logit link function,  
200 R Development Core Team, 2013) was used to explain the effect of subarea, patch and  
201 size of the patch on the proportion of seeds removed, with patch as a random factor and  
202 size as a fixed factor. Mean distance to nearest nest and mean nest density were used as  
203 covariates.

204

205 *Ant nest density* The study area was digitized and converted to a raster with a pixel size of  
206 20 cm. For each pixel, the average nest density (nests ha<sup>-1</sup>) and the distance to the nearest  
207 nest (m) were calculated. The average nest density was estimated using a spherical

208 Gaussian kernel centred around each pixel. The Gaussian kernel calculates a zone around  
209 a point and is defined by the bandwidth,  $\sigma$ . Minimising the mean-square error (Diggle,  
210 2003) yielded a value for  $\sigma$  of 5.7 m. However, this estimate was too large, resulting in  
211 the loss of too much detail of the spatial variation in ant nest density. An earlier study had  
212 yielded estimates of interaction zones (in which the probability of establishment of other  
213 nests is decreased) varying between 0.85 and 2.81 m, depending on nest size (Blanco-  
214 Moreno *et al.*, 2014). Here, we choose a value of 2.5 m for  $\sigma$ , which would  
215 approximately correspond to the estimated size of the interaction zone among large nests.  
216 This way, the bandwidth has biological relevance. The distance to the nearest nest was  
217 calculated as the distance from the centre of a pixel to the nearest nest. Next, for each  
218 seed patch the average nest density and the average distance to the nearest nest were  
219 computed as the mean of the values from the pixels included in the patch.

220 All analyses were performed in R (R Development Core Team, 2013), using the  
221 packages spatstat (Baddeley & Turner, 2005) and raster (Hijmans, 2014).

222

223

## 224 **Results**

225

226 Control patches contained  $30 \pm 5$ ,  $22 \pm 6$ , and  $85 \pm 8$  *Hordeum vulgare* L. seeds  $\text{m}^{-2}$  in  
227 subareas A, B, and C, respectively. Given these low numbers relative to the applied  
228 seeds, pre-existing seeds are not likely to have influenced seed removal rates. No ant  
229 species other than the harvester ant *M. barbarus* were observed. Previous studies found  
230 extremely low densities of granivorous carabids or rodents in the study area (Baraibar *et*  
231 *al.*, 2009). Considering that almost all patches were depleted before nightfall, we  
232 assumed that the only seed predator in the experiment was the harvester ant, *M. barbarus*.

233

### 234 *Seed removal rate*

235 The average sampling efficiency,  $\bar{E}$ , of the D-Vac was 93.8 % (range: 91.3 - 97.7  
236 %), which was used to correct further calculations to estimate seed removal. The lowest  
237 seed retrieval estimated for efficiency patches was 91.3%. So, the threshold seed removal



238 rate ( $Y$ ) was 8.7%. Patches with a seed removal rate lower than 8.7 % were considered  
239 undetected, and patches with higher values, as detected by harvester ants.

240

241 Seed removal rates were 97%, 86% and 98% for subareas A, B and C,  
242 respectively. Seed removal rate was lowest in small patches (78-94%) and highest in  
243 medium and large ones (86-100%) (Table 1). The size of the patch significantly  
244 influenced the seed removal rate (Table 2). On the other hand, the covariates mean  
245 distance to nearest nest and mean nest density did not have a significant effect on  
246 foraging. Seven patches had not been discovered by harvester ants ( $R < 8.7\%$ ) and only  
247 four patches had been partially exploited ( $8.7\% \leq R \leq 98\%$ ) (Table 1). All other patches,  
248 79 out of 90, had been fully exploited ( $R > 98\%$ ).

249

250 *Tables 1 and 2 near here*

251

252 Because the subareas were seeded sequentially, temperature differed between  
253 subareas. The average air temperature during the 24 h exposition was  $25.3 \pm 1$  °C in  
254 subarea A,  $20.4 \pm 1$  °C in subarea B and  $24.1 \pm 1$  °C in subarea C.

255

256 *Ant nest density and spatial distribution*

257 In figure 1, the average distance to the nearest nest is depicted for each point in  
258 the experimental area. The darker the shade of grey, the closer that point is to a nest.  
259 Similarly in figure 2, the average nest density, as calculated with a Gaussian kernel with a  
260 bandwidth of 2.5 m, is depicted for each point in the experimental area. Here, the darker  
261 the shade of grey, the higher the density of nests in the immediate vicinity of that  
262 particular point. In both figures, the location of seed patches (at scale) is indicated by the  
263 white squares. The size of the square is indicative of the size of the patch. Patches  
264 enclosed by circles with a solid line were not found ( $R < 8.7\%$ ); patches enclosed by  
265 circles with a dashed line were partially exploited ( $8.7 \leq R \leq 98$ ); patches without circles  
266 were fully exploited ( $R > 98\%$ ). Of the seven undiscovered patches two patches (both  
267  $0.25 \text{ m}^2$ ) were located in subarea A, four (three  $0.25 \text{ m}^2$  and one  $1 \text{ m}^2$ ) in subarea B, and  
268 one ( $0.25 \text{ m}^2$ ) in subarea C. The four patches that were only partially exploited were all

269 located in subarea B (two 0.25 m<sup>2</sup>, one 1 m<sup>2</sup> and one 9 m<sup>2</sup>) (Figures 1 and 2, dashed  
270 circles).

271

272

*Figures 1 and 2 near here*

273

274 The densities of ant nests were 416, 436 and 428 nests ha<sup>-1</sup> in subareas A, B and C,  
275 respectively. The nest density around seed patches that were fully exploited was, on  
276 average, two times higher than partially exploited patches or patches that were not found  
277 (Figure 3). The average distance to the nearest nest increased from patches that were fully  
278 exploited ( $2.3 \pm 0.7$  m), to patches that were partially exploited ( $3.2 \pm 0.6$  m) to patches  
279 that were not found ( $4.0 \pm 0.7$  m) (Figure 4).

280

281

*Figures 3 and 4 near here*

282

283 On average, seed patches that were not or partially exploited were located in areas with a  
284 lower ant nest density or a longer distance to nearest nest than seed patches that were  
285 fully exploited (Figures 1 and 2).

286

287

## 288 **Discussion**

289

290 In dryland cereal fields in NE Spain, the probability of finding a seed patch by harvester  
291 ants *M. barbarus* increased slightly, but significantly, with patch size. The reason was  
292 that seven of the smallest patches (0.25 m<sup>2</sup>) were not discovered ( $R < 8.7\%$ ), and four  
293 were only partially exploited ( $8.7\% \leq R \leq 98\%$ ). When a patch was found (79 overall), it  
294 was almost always fully exploited ( $R > 98\%$ ), resulting in very high seed removal rates,  
295 irrespective of patch size. Similar results have been found for the response of rodents to  
296 seed patches, with very high removal rates and no effect of patch size (Daedlow *et al.*,  
297 2014). The fact that patches were almost always fully exploited when found, can be  
298 explained by the high ant nest densities found in the field, and by the choice of the  
299 experimental design. The average nest density was 427 nests ha<sup>-1</sup>, which is high, but

300 normal for the region (Baraibar *et al.*, 2011c; range 140-1168 nests ha<sup>-1</sup>). Maybe for this  
301 reason, the covariates mean distance to nearest nest and mean nest densities were not  
302 significant. Results may have been different if nest density had been lower.

303

304 Seed patches that were partially exploited or not found were located in areas  
305 where the nest density was, on average, lower and the distance to the nearest nest larger  
306 than for patches that were fully exploited. This suggests that the location of a seed patch  
307 influenced the probability of being harvested by ants; seeds that are shed in an area where  
308 the ant nest density is low or the distance to the nearest nest is long have a lower  
309 probability of being collected. However, the duration of exposure to ants was very low in  
310 our trials. A 24 h exposure period had been chosen deliberately, because prior  
311 experiences had shown that prolonged exposure could result in extremely high encounter  
312 and exploitation rates (Baraibar *et al.*, 2011a), which would have masked any  
313 (temporary) differences caused by patch size or spatial distribution. However, under  
314 normal field conditions, exposure can last several weeks, which should suffice to  
315 annihilate any patch of any size.

316

317 A favourable location of a patch in the field (i.e. far away from ant nests) can  
318 increase the time during which seeds can disappear in the sub-soil, where they would be  
319 largely safe from foraging ants. Seeds are buried if, for example, they are transported by  
320 wind or rain into cracks or if they are covered by mud, dust or plant debris (Westerman *et*  
321 *al.*, 2009). Some weed species have developed mechanisms, such as hygroscoically  
322 active awns (Peart, 1979), with which the seeds slowly propel themselves into cracks and  
323 indentations in the soil. For such a burial mechanism time is essential.

324

325 Despite the fact that subarea B harboured the highest density of ant nests, it had  
326 the lowest predation rate, as more patches remained undiscovered and only this subarea  
327 harboured partially exploited patches. A lower average temperature during the time that  
328 the trial in subarea B was conducted could provide an explanation. The average air  
329 temperature during the period of seed exposure in subarea B had been 4-5°C lower than  
330 in the other two subareas. *Messor barbarus* is known to respond strongly to temperature

331 (Azcárate *et al.*, 2007). We noticed that some patches were discovered late, such that only  
332 part of the seeds had been harvested by the time of evaluation. Apparently, harvester ants  
333 in subarea B had been less active and had not enough time to find and fully exploit all  
334 patches.

335

336 The fact that oats seeds were used to estimate predation risk of weed seed raises  
337 the question whether harvester ants could pose a threat to crop seeds. A study conducted  
338 in 34 commercial winter cereal fields (Baraibar *et al.*, 2011b), indicated that both losses  
339 during crop sowing (0.2%) and close to crop harvest (0.6%) were extremely low.  
340 Occasionally higher losses were recorded (max. 9.2%) and these were caused by a longer  
341 exposure period of the cereals to the ants, and more mature cereal grains. Measuring  
342 losses of crop seeds was expressly not the purpose of this study. Instead, we used oats  
343 seeds as an easily available and easily manageable surrogate to weed seeds. Predation  
344 rates of oats seeds are comparable to those previously reported for weed seeds.  
345 Combining the results of Baraibar *et al.* (2011b) with our results shows that crop yield  
346 losses caused by *M. barbarus* are insignificant and more than offset by the benefits  
347 provided by the destruction of weed seeds.

348

349 In summary, the spatial distribution of harvester ant nests is such that not all seed  
350 patches have an equal probability of being found by harvester ants. Weed seeds may have  
351 more time to experience lower predation, if patches are isolated from ant nests, mostly  
352 small ones. This, in turn, could influence the spatial distribution of weed patches in  
353 dryland cereal fields in NE Spain. This raises the interesting question whether it might be  
354 possible to decrease the survival probability of weed seed patches by managing the level  
355 and spatial distribution of ant populations? To achieve that, it would be necessary to  
356 identify the key factors determining the spatial arrangement of the colonies. A previous  
357 study indicated that the origin of spatial trends (4-12 m) should be sought in biotic  
358 factors, such as seed availability, intraspecific competition or the distribution of landing  
359 sites of founding queens (Blanco-Moreno *et al.*, 2014). Understanding these factors  
360 would be instrumental in developing strategies to manage harvester ants populations and  
361 enhance the level of biological control exerted on weed populations.

362

363

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365

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450 Tables

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452 Table 1. Average seed removal rate,  $R$  (based on seed weight), number of patches not  
 453 found\* ( $R < 8.7$ ), partially exploited ( $8.7 \leq R \leq 98$ ) and fully exploited ( $R > 98\%$ ) by  
 454 harvester ants for four patch sizes in subareas A, B and C

455

Subarea	Patch size class	$N$	Average $R$ [%]	Number of patches with		
				$R < 8.7^*$	$8.7 \leq R \leq 98$	$R > 98$
A	0.25 m <sup>2</sup>	16	88 ± 9	2	0	14
	1 m <sup>2</sup>	8	100 ± 0	0	0	8
	3 m <sup>2</sup>	4	100 ± 0	0	0	4
	9 m <sup>2</sup>	2	100 ± 0	0	0	2
B	0.25 m <sup>2</sup>	16	78 ± 10	3	2	11
	1 m <sup>2</sup>	8	82 ± 13	1	1	6
	3 m <sup>2</sup>	4	100 ± 0	0	0	4
	9 m <sup>2</sup>	2	86 ± 9	0	1	1
C	0.25 m <sup>2</sup>	16	94 ± 6	1	0	15
	1 m <sup>2</sup>	8	100 ± 0	0	0	8
	3 m <sup>2</sup>	4	100 ± 0	0	0	4
	9 m <sup>2</sup>	2	100 ± 0	0	0	2

456 \* The lowest efficiency found in a patch (91.3%) was used to derive the threshold value  
 457 (8.7%) below which patches were assumed not to have been found and exploited by ants  
 458 (see Material and Methods).

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470 Table 2. Analysis of deviance for the effect of patch size and subarea on the proportion of  
471 seeds removed by harvester ants in a cereal field, with mean distance to nearest nest and  
472 mean nest density as covariates (glm, quasi-binomial distribution, logit-link function).

473

Subarea	Effect	mean deviance	deviance ratio	<i>P</i>
Fixed effects				
	subarea	0.208	51.459	0.609
	size	3.661	47.792	0.021
	subarea*size	0.001	38.964	0.883
Random effects				
	patch	0.0000	47.792	
	residual	51.661		
Covariates	Mean distance to nearest nest	8.111	39.680	0.378
	Mean nest density	0.716	38.964	0.324

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