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1 **Evidence of high individual variability in seed**
2 **management by scatter-hoarding rodents: Does**
3 **‘personality’ matter?**

4

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17

18 **Abstract.-** The predation and dispersal of seeds by scatter-hoarding animals is one of the most
19 studied processes in the context of animal-plant interactions. The seed management by these
20 animals has been traditionally approached at the population level, assuming that the patterns
21 documented in field are similar among all individuals of the population, and considering the
22 variability within the population as random noise. However, little is known about to what extent
23 this variability responds to different and consistent behavioural displays among individuals. The
24 aim of this study was to analyse the individual variation and consistency in behaviour by
25 scatter-hoarding rodents within a population. As model we used the wood mouse (*Apodemus*
26 *sylvaticus*), a key disperser of holm oak acorns (*Quercus ilex*) that, in turn, suffers a high
27 predation pressure by the common genet (*Genetta genetta*). In two sets of laboratory
28 experiments, we compared the variance and consistency in behavioural displays and acorn
29 managing generated by the individual differences with that generated by the manipulation of the
30 perceived predation risk using scents of genets. Genet scents reduced the activity (i.e. time out
31 of the refuge) in all rodents, but the differences and the consistency in activity among
32 individuals accounted for the 82.5% of total variance. Also, rodents showed different and
33 consistent displays of stressed or relaxed behaviours. More than 87% of variance in seed
34 managing variables, like dispersal distance and seed size selection, was explained by consistent
35 differences among individuals across scent treatments. The increase of stressed behaviours and
36 decrease of relaxed ones were positively related with the dispersal ability (i.e. longer distances
37 and larger acorns). Our study highlights the importance of considering the individual component
38 of behaviour in scatter-hoarding rodents. This fine-scale level, largely overlooked in the
39 ecological framework, will help to increase our understanding on seed management by scatter-
40 hoarding animals.

41 **Keywords:** individual variation; personality; predation risk; scatter-hoarding rodent; seed
42 dispersal.

43

44 Plants and animals have coevolved in many complex interactions, ranging from
45 antagonisms, such as herbivory, to mutualisms, such as seed dispersal (Labandeira, 2002). The
46 outcome of these interactions depends on many factors from both sides, and can be approached
47 under different perspectives (e.g. evolutionary, ecological, and behavioural). Seed management
48 by scatter-hoarding animals is one of the most studied processes in the context of animal-plant
49 interactions, because of the dual behaviour displayed by these animals (Herrera & Pellmyr,
50 2002; Vellend et al., 2006; Schupp et al., 2010). On the one hand, they consume seeds, having a
51 negative impact on plant populations, but they can also move and store seeds in certain sites that
52 may favour seed dispersal and seedling recruitment, thus having a positive effect in plant
53 recruitment (Vander Wall, 1990; Herrera, 2002; Gomez et al., 2008; Muñoz & Bonal, 2011;
54 Sunyer et al., 2015). This dual role and its outcome for plants has an important behavioural
55 dimension, as it depends on individual decisions of scatter-hoarding animals (Muñoz & Bonal,
56 2008a, 2008b; Perea et al., 2011; Sunyer et al., 2013, 2015). Understanding the nature of these
57 decisions may help to shed light on seed fate and ultimately into plant populations and
58 community dynamics (Herrera & Pellmyr, 2002; Vellend et al., 2006; Schupp et al., 2010).
59 Moreover, the study of seed dispersal has increased in recent years, probably due to the rising
60 concern about the survival of numerous plant species in the context of global change (Robledo-
61 Arnuncio et al., 2014).

62 Many factors are known to influence animal choices through the decision-making
63 process. For example, the seed choices of scatter-hoarding rodents are influenced by physical
64 characteristics of food, such as seed size and shape (Bonfil, 1998; Gómez, 2004; Preston &
65 Jacobs, 2009; Muñoz et al., 2012; Sunyer et al., 2015). Most studies have documented that
66 dispersers prefer larger seeds because of their higher nutrient content (Jansen et al., 2004; Xiao
67 et al., 2004; Muñoz & Bonal, 2008a), but their choices may also depend on the costs of handling
68 and moving the larger seeds (Kerley & Erasmus, 1991; Muñoz & Bonal, 2008b, Muñoz et al.,
69 2012). The cost of handling and carrying seeds can be particularly high for scatter-hoarding
70 rodents, as they are usually prey of a huge variety of terrestrial and aerial predators, so that the
71 perceived predation risk is known to influence their seed preferences and management (Leaver,

72 2004; Sunyer et al., 2013; Navarro-Castilla & Barja, 2014; Heinen-Kay et al., 2016). Also, the
73 perceived risk of pilferage by conspecifics can influence seed management by scatter-hoarding
74 rodents (Hopewell & Leaver, 2008; Steele et al., 2008; Muñoz & Bonal, 2011; Samson &
75 Manser, 2016)

76 The patterns of seed predation and dispersal by scatter-hoarding rodents have been
77 traditionally approached at species or population level (e.g. Hollander & Van der Wall, 2004;
78 Muñoz & Bonal, 2007; Schupp et al., 2010; Perea et al., 2011; Xiao et al., 2013). That is, the
79 responses of rodents to seed characteristics and environmental factors are often assumed to be
80 the same among all individuals within a given species or population. Thus, a lot of studies have
81 focused on the environmental causes of behaviour (i.e. exogenous), such as seed traits, mast
82 seeding, pilferage and predation risk, etc., providing means and deviances for variables of seed
83 management like predation / dispersal rates, seed size, dispersal distances, cache management,
84 for different species and populations worldwide (Muñoz & Bonal, 2007; Gómez et al., 2008;
85 Schupp et al., 2010; Perea et al., 2011; Xiao et al., 2013). These kind of studies assumes the
86 behavioural variability among individuals within the population or species as random noise;
87 however, little is known about to what extent these deviations are random or respond to
88 different and consistent patterns of behaviour among individuals within the same population
89 (i.e. endogenous causes of behaviour). Probably, one of the main reasons of this lack of
90 information has been the methodological difficulties to focus in detail on the behavioural
91 displays and seed management in field at the individual level, because scatter-hoarding rodents
92 are usually small, nocturnal and very sensitive to potential predators.

93 In recent years, the study of animal personality has become a hot topic under an
94 evolutionary and ecological framework (Réale et al., 2007, 2010; Wolf et al., 2007; Stamps &
95 Groothuis, 2010; Wolf & Weissing, 2012; Carter et al., 2013; Moran et al., 2016; Pennisi,
96 2016). The idea that different individuals of the same population show different, but consistent,
97 behavioural patterns is appealing, especially for scatter-hoarding species in the context of
98 animal-plant interactions. To the best of our knowledge, no study has analyzed in detail the
99 variation in individual behaviour and consistency in seed management by scatter-hoarding

100 rodents. Thus, the aim of this study is to analyse the extent of this individual variation and the
101 consistency in behaviour by scatter-hoarding rodents within a population, in order to discuss the
102 role of individual patterns in the observed patterns of seed management (i.e. predation and
103 dispersal of seeds). We specifically assessed how the behavioural variance generated by the
104 individual component was comparatively higher than that generated by an important
105 environmental factor like the perceived predation risk.

106 As a study model we have used a well-documented plant-disperser-predator
107 assemblage: holm oak (*Quercus ilex*) acorns, which are consumed and dispersed by wood
108 mouse (*Apodemus sylvaticus*), that in turn is the main prey of the common genet (*Genetta
109 genetta*). The wood mouse is the most abundant scatter-hoarding rodent in Mediterranean areas
110 of southern Europe, distributed from the Iberian Peninsula to southwestern Asia and the
111 Himalayas, and from northwestern Africa to the south of Scandinavia (Torre et al., 2002;
112 Urgoiti et al., 2018). This nocturnal and small rodent (15-35g) is a prominent consumer and
113 disperser of acorns during the seeding season in autumn, influencing the recruitment dynamics
114 of many oak species (den Ouden et al., 2005; Sunyer et al., 2015), like the holm oak, which is
115 the most widespread oak in the Mediterranean basin (Blondel & Aronson, 1999). This oak
116 shows an extraordinary variability in acorn size (from less than 1 g to more than 15g, Muñoz
117 & Bonal, 2008b). In Mediterranean areas, the wood mouse is the most abundant prey (up to
118 86.9% of biomass diet) of the common genet, *Genetta genetta*, a common nocturnal carnivore
119 (Virgós et al., 1999; Torre et al., 2003). In fact, the wood mouse is able to detect and respond to
120 the scents of genets in order to reduce the predation risk when foraging acorns in autumn
121 (Sunyer et al., 2013). Using this oak-rodent-carnivore system, we performed two series of
122 laboratory experiments with a wild population of wood mice: one to characterise and analyse in
123 detail the individual behaviour, and other to assess individual seed management of holm oak
124 acorns. In both sets of experiments, we manipulated experimentally the perceived predation
125 risk, using genet scents, to assess its effects on rodent behaviour. We hypothesised that, if the
126 individual component of behaviour was relevant, rodents would display different, but

127 consistent, individual behaviours and patterns of seed management, even under different levels
128 of perceived predation risk.

129

130

131 **METHODS**

132 *Capture and Maintenance of Rodents*

133 We captured 25 adult wood mice (mean weight \pm SE: 19.5g \pm 3.4, range: 12-26g) in the
134 forest of Can Balasc (Collserola Natural Park; 41° 24' N, 2° 6' E, Barcelona, Spain) a natural
135 reserve representative of Mediterranean oak forests dominated by the holm oak (95% of the
136 forest area according to Espelta et al., 2009). In this area, the rodent community is mainly
137 composed of wood mice (99%), which share the habitat with the common genet (Sunyer et al.,
138 2013). Rodents were captured from March to April 2017 in a surface of 2 ha using Sherman
139 live-traps (23.5 \times 8 \times 9 cm; HB Sherman Traps Inc., Tallahassee, Florida USA) baited with a
140 mixture of flour and tuna in oil and a piece of apple for hydration. Additionally, they contained
141 a handful of hydrophobic cotton so that the captured rodents could make a nest to remain
142 protected (Muñoz et al., 2009; Sunyer et al., 2014).

143 Captured rodents were carried out to the laboratories of the Can Balasc field research
144 station in their provisional nests made inside the traps. All captured rodents were then weighed
145 and housed individually indoors in terraria (30 x 30 x 35 cm) filled with a layer of sand of 5 cm
146 deep to provide traction for rodent stepping and facilitate the movement. We also included a
147 refuge (10 x 16 x 8 cm) with a piece of waterproof cotton to mimic their natural nests made in
148 field burrows in order to feel safe and protected. These home-terraria were placed indoors under
149 natural photoperiodicity and no visual contact among individuals to avoid stress. The home-
150 terraria were not open, but had a cover with several slits to provide ventilation, in order to
151 reduce the probability that experimental rodents could detect scents from other rodents. We
152 provided apple and hamster food as food source (Vitacraft Premium Menu), a high quality

153 natural food, made with seeds, cereals, and greens, that offers a complete daily menu for
154 rodents. Rodents were kept in the laboratories on average for 18 days, including habituation and
155 trials (range 15-22).

156

157 *Experimental Design*

158 After 3 days for habituation to the individual home-terraria, we performed two types of
159 experiments with all captured rodents. Experiment one was conceived to characterise the
160 individual behaviour and experiment two to analyse individual acorn management.

161

162 *Characterisation of individual behavior experiments*

163 This experiment consisted of three trials per individual in order to analyse the
164 differences in behaviour among individuals and its consistency within each individual. These
165 experiments consisted of recording the activity and detailed behaviour of each individual with
166 nocturnal video cameras in its home-terraria during three nights (*i.e.* trials) under different scent
167 treatments: (1) a control trial, (2) a predator scent trial and (3) a control after predator scent trial.

168 We attached to the ceiling of each home-terraria three cotton discs (5.5 cm) that were
169 soaked with the stimulus according to the scent treatment: distilled water for the two control
170 trials, and genets' scent for the predator trial. Genets' scent was obtained from 10 g of fresh
171 feces collected in latrines located in the study area, which were thawed and mixed with 30 ml of
172 water to obtain an homogeneous mixture which serves rodents as a cue of predator presence
173 (Sunyer et al., 2013). Genet feces are indeed a powerful source of chemical signals for other
174 animals, as the scents secreted by perineal glands are mixed with feces and deposited in latrines,
175 which serve as stations for scent communication, playing a role in territoriality, sexual
176 attraction, warning, etc. (Espirito-Santo et al. 2007). Cottons were placed at 19:00 GMT and we
177 set-up one night-vision cameras for each individual, which recorded continuously during 10h
178 (from 21:00 to 07:00 GMT) under natural photoperiodic conditions. Before each trial, we

11

12

179 removed all the remaining food of the home-terrarium (checking especially the nest) except a
180 piece of apple that was placed outside the nest with plastic gloves.

181 Based on the recordings obtained from the three trials, we analysed in detail the
182 behaviour of each experimental rodent. We displayed the video recordings in Microsoft
183 Windows Media Player (Microsoft®) in slow motion (x 0.5) to ensure an accurate measurement
184 of behavioural variables. For each trial, we first measured the ‘total activity’ as the percent of
185 the total time spent out of the refuge, which is usually taken as part of the boldness score of the
186 individuals (Carter et al., 2013; Mamuneas et al., 2015; Yuen et al., 2015). Then, we analysed in
187 detail a sample of 25 min randomly taken from the total activity time spent out of the refuge for
188 each individual and trial. This sample was used to categorise the behaviours displayed by each
189 individual as ‘stressed’ or ‘relaxed’. Stressed behaviours included ‘vigilance and freezing’
190 (standing still on their back feet or remaining completely immobile), ‘trying to escape’
191 (jumping, clambering or climbing), and ‘taking and shatter the cotton discs soaked with the
192 stimulus’. Relaxed behaviours included ‘sniffing’, ‘feeding or handling the piece of apple’,
193 ‘self-grooming’ (cleaning itself) and ‘burrowing or digging’ (Apfelbach et al., 2005; Sunyer et
194 al., 2013). Neutral behaviours, such as moving slowly along the terraria, were not included as
195 stressed or relaxed. Once categorised, the proportion of relaxed and stressed behaviors was
196 calculated for each individual and trial.

197

198 *Seed Management Experiments*

199 The seed management experiments consisted of two consecutive trials per individual
200 conducted in indoor arenas (134 x 92 x 75 cm): in the first experiment water was sprayed along
201 the arena (i.e. control treatment) and the second one the scents of genets were sprayed along the
202 arena (i.e. predator treatment). In each trial, each rodent was provided with 6 holm oak acorns
203 that were classified in 3 categories of size, in order to analyse the effects of acorn size on rodent
204 preferences: 2 small acorns (< 3 g), 2 medium acorns (3-4.5 g) and 2 large acorns (> 4.5 g).

205 Fresh acorns were collected from oaks during January 2017 and maintained at 4°C until the
206 experiments. In one corner of the arena we placed the own nest of the experimental rodent
207 (taken from the home terrarium) and in the opposite corner the 6 acorns randomly located in a
208 2×3 grid with a distance of 5 cm among them.

209 Two hours before each trial, we removed the remaining food from the nest with plastic
210 gloves, to ensure that experimental acorns were the only source of food available. Rodents and
211 experimental acorns were weighed before and after each trial (to the nearest 0.01 g). Each wood
212 mouse was placed in the arena at 17:00 GMT only with its home refuge in order to leave some
213 time for conditioning. Then, we positioned the acorns and sprayed the stimulus treatment at
214 18:30 GMT. Acorns were manipulated using fresh gloves to avoid effects of human odour cues
215 on rodent choices (Wenny, 2002). After each trial, the arenas were cleaned thoroughly to avoid
216 scent contamination among trials.

217 Digital video cameras with night vision were installed over the arenas and in each trial
218 we video recorded for 13 h (between 19:00 and 08:00 GMT) to monitor the behaviour of each
219 individual during the trial. Experimental acorns were revised at 08:00 GMT, noting the distance
220 moved and whether each acorn had been partially or completely predated. We analysed the
221 video recordings of seed management in Microsoft Windows Media Player (Microsoft®) in
222 slow motion (x 0.5) and also calculated the ‘total activity’ as the percent of the time spent out of
223 the nest with respect to the total time.

224

225 *Data Analysis*

226 In the behavioural characterisation experiments, we assessed the effects of the predator scent
227 treatment on rodent behaviour using repeated-measures ANOVAs, with total activity (i.e.
228 percentage of time out of the refuge) and the proportion of stressed-relaxed behaviours as
229 dependent variables. We also checked the differences between the two control trials (previous
230 and post-genet scents) to assess whether the predator effects were fixed or not in rodents after

231 the predator scent treatment. We analysed the differences in behaviour among individuals, and
232 the consistency within individuals across treatments, with a model that estimated the
233 components of variance, with the “individual rodent” as random factor and “scent treatment”
234 (i.e. control, predator and control after predator) as fixed factor. These analyses provide the
235 proportion of behavioural variance explained by each factor. We used regression models to
236 analyse the potential effects of rodent weight on the individual variance in behavioural patterns.

237 In the seed managing experiments, we also analysed the effects of ‘individual’ and scent
238 treatment’ using a model that estimated the components of variance, with the “individual
239 rodent” as random factor and “scent treatment” as fixed factor. In this case, the dependent
240 variables were: ‘activity’ (percentage of time spent outside the refuge), ‘dispersal distance’ (Σ
241 distances of seeds moved during the trial), ‘seed size’ (mean weight of the seeds moved during
242 the trial), ‘ratio’ (mean weight of the seeds moved during the trial divided by the weight of the
243 experimental rodent, see Bonal & Muñoz, 2008b), ‘dispersal effort’ (Σ weight of seeds moved *
244 distance moved). We used regression models to assess whether the activity of each rodent in the
245 seed managing trials was consistent with the activity recorded in the behaviour characterisation
246 trials, and to what extent seed management was related to the stressed and relaxed behaviours.
247 The comparisons between sexes were not possible given that we just captured 4 females out of
248 the 25 experimental rodents. However, we have previously demonstrated that the sex of wood
249 mice has no effects on seed management (Muñoz & Bonal 2008b).

250

251 *Ethical Note*

252 In this research, we captured 25 adult wood mice (*Apodemus sylvaticus*) using Sherman live-
253 traps (23.5 × 8 × 9 cm; HB Sherman Traps Inc., Tallahassee, Florida USA) in the Collserola
254 Natural Park (41° 24' N, 2° 6' E, Spain) that were used in the experiments of behaviour. We also
255 captured one pregnant female and four juveniles, but they were immediately released. Traps
256 were baited with a piece of apple and a handful of hydrophobic cotton. These traps do not
257 produce any injury to rodents and allow them to make a nest inside with the piece of cotton

258 provided, which helps rodents to feel safe and relaxed during the capture period (Muñoz et al.,
259 2009; Sunyer et al., 2013, 2016). The piece of apple (ca. 10g) ensures enough individual
260 hydration during the capture period, as the piece is never totally consumed. Traps were daily
261 checked at dawn, so that rodents were inside the traps just 6-8 hours at most. No lactating
262 females were caught during the trapping sessions. Capture, handle and maintenance of wood
263 mice authorization was issued by the Generalitat de Catalunya (Departament de Territori i
264 Sostenibilitat; reference SF/156) after approval by the advisory committee of the Collserola
265 Natural Park authorities. All the handling and sampling were done by M.F-R., who holds the
266 EU permit for experimentation with animals authorised by the French Ministry of Agriculture
267 and Fisheries (authorization reference R45GRETA110). Wood mice capture and management
268 in the laboratory adhered to the ASAB/ABS Guidelines for the Use of Animals in Research.
269 During this research no rodent resulted injured and all were healthy until the experiments
270 finished, when rodents were released at the exact point of capture.

271

272

273 **RESULTS**

274 *Characterisation of Individual Behaviour*

275 Predator scent reduced significantly the activity (i.e. proportion of time outside the
276 refuge) of rodents from the control to the predator scent trials (repeated-measures ANOVA: $F_{1,22}$
277 = 4.83, $P = 0.038$). Yet, the activity did not differ between the two control trials (before and
278 after the trial of predator scents; repeated-measures ANOVA $F_{1,22} = 0.04$, $P = 0.85$). Hence,
279 experimental rodents adjusted their activity (i.e. time exposed to predators) to the predation risk
280 perceived in each moment, lacking “preventive behavior” after a contact with predator scents.
281 More interestingly, the time expended by rodents out of the refuge was extremely variable
282 among rodents, from 42 min to 5 h and 23 min (out of 9 h of video recordings per individual),

283 and this time was extraordinarily repeatable within the same rodent across different trials (Table
 284 1).

285

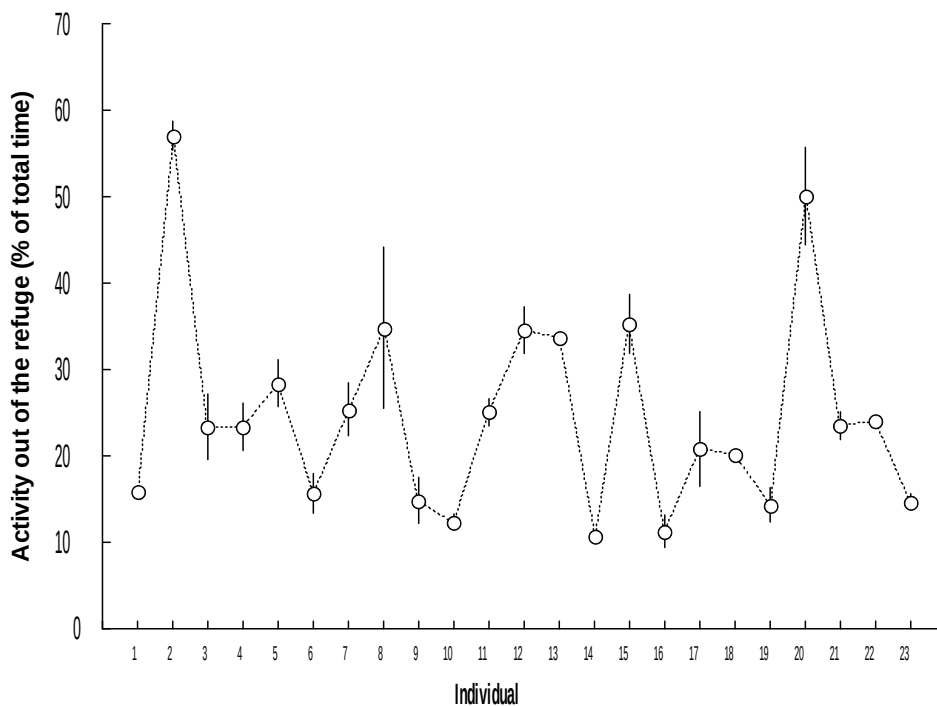
286 **Table 1.** Behavioural patterns of experimental rodents in the characterisation trials.

Trial	% time outside the refuge (n=23)		% stressed displays (n=23)		% relaxed displays (n=23)	
	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
Control	25.8 ± 2.7	10.7 – 59.2	23.2 ± 3.5	2.9 – 56.5	46.0 ± 4.8	6.0 – 79.8
Predator scent	22.9 ± 2.3	7.7 – 58.1	24.8 ± 3.2	6.0 – 57.9	44.6 ± 3.8	9.8 – 72.1
Control 2	25.5 ± 2.9	10.7 – 59.3	31.7 ± 4.2	6.3 – 75.7	40.6 ± 3.8	6.9 – 77.0

287 Mean, Standard Error (SE) and range of the behavioural displays (proportion of time expended by
 288 experimental individuals out of the refuge and proportion of stressed and relaxed behaviours)
 289 displayed during the three behaviour characterisation trials: control, predator scent and control
 290 after predator scent (control 2)

291

292 The model for estimating the components of variance showed that the individual
 293 differences were highly significant (factor individual: $F_{22,44} = 15.16$, $P < 0.0001$; Figure 1), and
 294 explained the 82.5% of total variance in activity out of the refuge, a high variance compared
 295 with that generated by the scent treatment (Table 1). These different and fixed patterns of
 296 activity among rodents were not related to rodent weight in any of the scent treatments (Control:
 297 $\beta = -0.21$, $F_{1,21} = 0.95$, $P = 0.34$; Predator: $\beta = -0.21$, $F_{1,21} = 0.98$, $P = 0.33$; Control after
 298 predator: $\beta = -0.08$, $F_{1,21} = 0.14$, $P = 0.71$).



299

300 **Figure 1.** Differences among rodents in the proportion of time spend out of the refuge (of the
 301 total recorded) during the behaviour characterisation trials across the three scent treatments.
 302 Mean (points) and SE (lines) for the pooled data of the three trials performed by each
 303 individual.

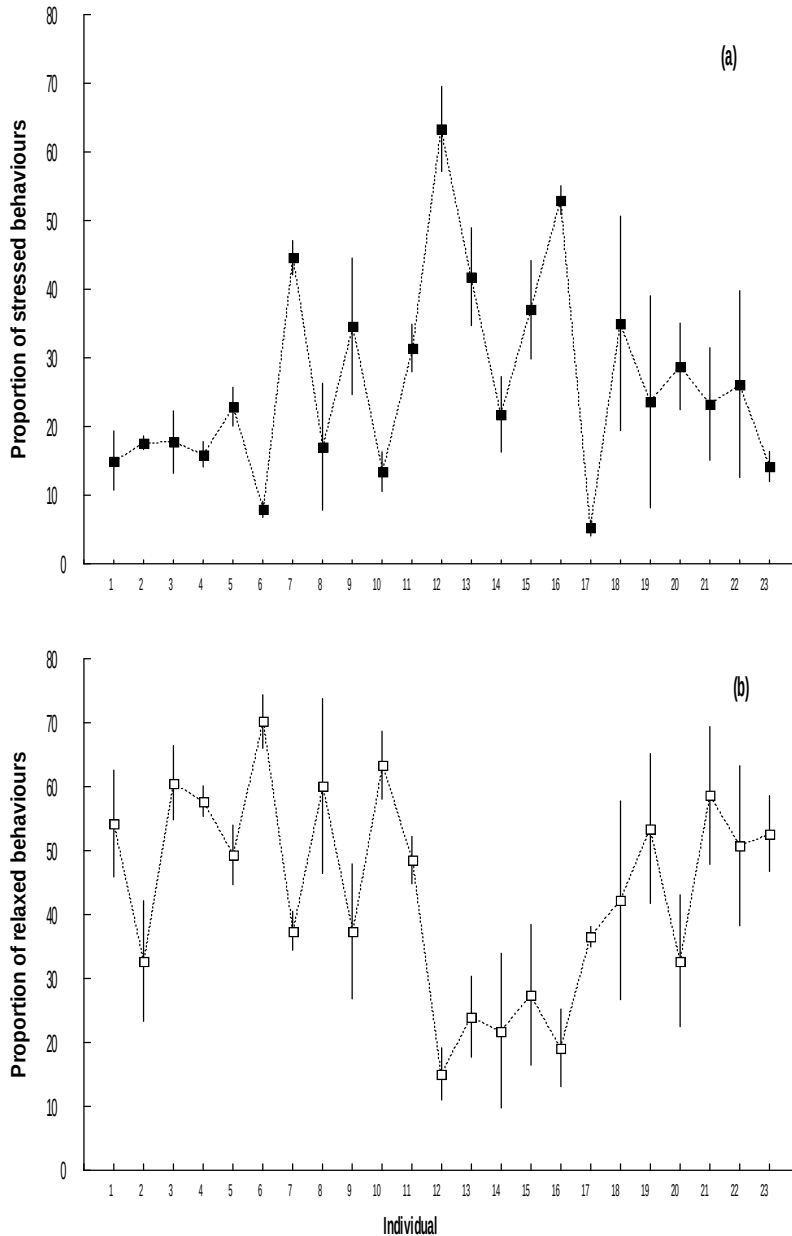
304

305 The proportion of relaxed and stressed behaviours did not correlate with the time
 306 expended by individuals outside the refuge in any scent treatment ($P > 0.3$ in all cases). Indeed,
 307 although predator scents reduced individual's activity (i.e. the time exposed out of the refuge),
 308 they did not change the type of behavior displayed once individuals decided to leave the shelter,
 309 so that the proportion of stressed and relaxed behaviors did not differ significantly between the
 310 control and predator experiments (repeated-measures ANOVA: stress $F_{1,22} = 0.36$, $P = 0.55$;
 311 relax $F_{1,22} = 0.17$, $P = 0.68$, Table 1). However, the variance in proportion of stressed or relaxed
 312 behaviours was mainly explained by individual differences and it was very consistent for each
 313 individual across treatments, as in the case of the activity time. The factor individual explained
 314 52.3 % of the total variance in stressed behaviors and 42.2% in relaxed behaviors (individual
 315 effect: stress: $F_{22,44} = 4.28$, $P < 0.001$; relax $F_{22,44} = 3.19$, $P < 0.001$; Figure 2). The proportion of

23

24

316 stressed and relaxed behaviours were inversely correlated ($\beta = -0.75$, $F_{1,67} = 88.42$, $P < 0.0001$),
 317 and these behaviors did not correlate with rodent size in any of the three scent treatments ($P >$
 318 0.2 in all models). Thus, the behaviour characterisation trials revealed that rodent behaviour
 319 shows a strong individual component, accounting for most behavioural variation in the
 320 population of experimental individuals as compared to the variance generated by the scent
 321 environment (i.e. perceived predation risk).



322

323

324 **Figure 2.** Differences among rodents in the proportion of different type of behaviour -stressed
 325 (a) and relaxed (b)- displayed out of the refuge during activity trials. Mean (squares) and SE
 326 (lines) for the pooled data of the three trials performed by each rodent.

25

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327

328 *Seed Managing*

329 The activity of each individual in the arenas during the seed managing trials (i.e.
330 proportion of time active) was positively correlated with the time out of the refuge measured in
331 the behaviour characterisation trials (i.e. home-terraria; $\beta = 0.52$, $F_{1,16} = 6.09$, $P = 0.025$). The
332 variance among individuals in the patterns of seed management and the consistency within each
333 individual between scent treatments were extraordinarily high, so that most variance in seed
334 management was explained by inter-individual differences, and not by the presence of predator
335 scents (Table 2).

336

337 **Table 2.** Repeatability and individual variability among experimental rodents in seed
338 management.

	β	t	d.f.	P	Var. indiv.	Predator effect
Activity ⁽¹⁾	0.84	6.63	18	<0.001	87.5 %	$F_{1,19} = 0.39$, $P=0.53$
Seed size ⁽²⁾	0.39	2.05	23	0.05	33.0 %	$F_{1,24} = 0.04$, $P=0.84$
Ratio ⁽³⁾	0.66	4.24	23	<0.001	66.3 %	$F_{1,24} = 0.26$, $P=0.61$
Disp. Dist. ⁽⁴⁾	0.78	5.78	23	<0.001	76.7 %	$F_{1,24} = 1.03$, $P=0.32$
Disp. Effort ⁽⁵⁾	0.81	6.59	23	<0.001	80.7 %	$F_{1,24} = 0.74$, $P=0.39$

339 Correlations between the two seed management trials (control vs. predator scent) in the
340 variables (1) activity time in the arenas (2) size of seeds dispersed (3) size of seeds
341 dispersed/rodent size (ratio) (4) dispersal distance and (5) dispersal effort (see data analyses).
342 The proportion of variance explained by the factor “individual” (Var. indiv.) and the predator
343 scent effects are showed.

344

345 The activity time measured in the behaviour characterisation trials was not related to the
346 variables of seed managing, but the proportion of stressed and relaxed behaviours was
347 significantly related to different variables of seed management (Table 3). The increase of
348 stressed behaviours and the decrease of relaxed behaviours were positively related to the
349 dispersal effort (Table 3). This was especially relevant for the dispersal distances of seeds which
350 significantly increased with the proportion of stressed displays and significantly decreased with
351 the proportion of relaxed displays (Table 3). Also, the size of seeds moved decreased

27

28

352 significantly with the proportion of relaxed displays so that more relaxed individuals preferred
 353 smaller seeds (Table 3).

354

355 **Table 3.** Relationship between behavioural displays and seed management.

	Activity time			Stressed displays			Relaxed displays		
	β	t_{44}	P	β	t_{44}	P	β	t_{44}	P
Dispersal effort	-0.05	-0.32	0.74	0.37	2.66	0.010	-0.39	-2.80	<0.01
Disp. Distance	-0.06	-0.40	0.69	0.38	2.73	<0.01	-0.32	-2.21	0.03
Seed size	0.11	0.73	0.47	0.17	1.14	0.26	-0.30	-2.06	0.04

356 Relationships between the behavioural displays measured in the behaviour characterisation
 357 trials (activity time, proportion of stressed and relaxed displays) and the variables measured in
 358 the seed managing trials (Dispersal effort, dispersal distance and size of the seeds moved).

359

360 DISCUSSION

361 We found strong and consistent inter-individual differences in the behavioural patterns of
 362 a scatter-hoarding rodent species, so that the differences among individuals account for most
 363 behavioural variance compared to the variance generated by the experimental manipulation of
 364 environment using scents of genets (i.e. perceived predation risk). We found an effect of the
 365 predator scents on rodent activity during the behavioural characterisation trials, suggesting that
 366 the wood mouse is able to detect and respond to genet scents by reducing their activity, as has
 367 been previously reported for other species (Grabowski & Kimbro, 2005; Verdolin, 2006; Jolles
 368 et al., 2015, see Sunyer et al., 2013 for the wood mouse). However, this reduction in activity
 369 was negligible in comparison with the consistent variability in the activity among individuals
 370 (more than 80% of total variance). These results suggest a prevalence of the endogenous causes
 371 of behaviour (i.e. individual) over the exogenous ones (i.e. environmental). The patterns of seed
 372 management were also extraordinarily variable among individuals and very repeatable within
 373 the same individual across the scent treatment. For example, more than 75% of variation in seed

374 dispersal distances, and more than 80% of variation in dispersal effort (Σ weight of seeds moved
375 * distance moved) were explained by consistent differences among individuals. Overall, more
376 than 87% of variance in activity in seed managing experiments was explained by consistent
377 individual differences. Hence, basic foraging decisions like ‘what seed to eat or to move’, or
378 ‘how far to move seeds’, probably have a strong individual component. This component seems
379 to be related with the differences in the proportion of stressed/relaxed behaviours observed
380 among experimental rodents, so that more stressed individuals showed a better ability for
381 moving seeds (with longer dispersal distances and higher dispersal effort) than relaxed ones.
382 This suggests that the level of stress increases the foraging investment and performance of
383 scatter-hoarding rodents at the early stages of seed choice and seed movement, allowing them to
384 hoard larger seeds further away from the seed source to prevent pilferage (Muñoz & Bonal,
385 2011). The level of relax, by contrast, seems to reduce the foraging efficiency by enhancing the
386 movement of seeds at shorter distances, and to increase the movement of smaller seeds, which
387 have a lower nutrient value (Kerley & Erasmus, 1991), and that ultimately represent a lower
388 dispersal effort (Muñoz & Bonal 2008b). These results agree with previous studies suggesting
389 that the stress level may enhance foraging efficiency in small rodents (Chaby et al., 2015). The
390 specific mechanisms by which stress level affects foraging are not clear. One potential
391 explanation is that stressed individuals are probably more familiarised with the effects of the
392 stress response, and so they can function in a high arousal state more easily (Natelson et al.,
393 1988), allowing them to increase the foraging effort and performance when facing seeds.

394 The personality of animals is currently an appealing research field under an evolutionary
395 and ecological scenario (Réale et al., 2010; Stamps & Groothuis, 2010; Wolf & Weissing, 2012;
396 Carter et al., 2013; Pennisi 2016) since, in the last decades, a lot of studies have pointed to the
397 importance of considering consistent behaviours through time and conditions at individual level
398 (Verbeek et al., 1996; Hayes & Jenkins, 1997; Koolhaas et al., 1999; Sneddon, 2003; Muñoz &
399 Bonal, 2008a; Korpela et al., 2011). The concept of personality is complex and may be ruled by
400 genetic characteristics, physiological processes, environmental experiences, and their interaction

401 (Bell, 2005; Nussey et al., 2007; Sih & Bell, 2008; Dosmann et al., 2015). Our experiments do
402 not allow disentangling to what extent the individual differences respond to different individual
403 experiences in the field or, by contrast, they have a more innate basis (e.g. genetic,
404 physiological). However, it is known that cognitive processes, such as learning or memory, are
405 exceptionally well developed in scatter-hoarding rodents (Pan et al., 2013), and that they use
406 their own experiences to adjust individual foraging decisions like seed management (Muñoz &
407 Bonal, 2008a; Yi et al., 2016). In scatter-hoarders, these cognitive abilities may be evolutionary
408 advantageous in order to improve the recovery of cached seeds or to avoid cache pilferage
409 (Muñoz & Bonal, 2011; Yi et al., 2016), and might also promote the different strategies and the
410 consistent individual patterns of behaviour we have found in the current study.

411 The study of the patterns of seed predation and dispersal by scatter-hoarding rodents has
412 been traditionally approached from a population scale. That is because experimental designs
413 usually consist of marking and placing seeds in field plots in order to monitor seed fate after
414 predation or dispersal, with no possibility of controlling the number and identity of scatter-
415 hoarders visiting each seed plot. Using such methodological approach, most studies have tested
416 how the patterns of predation and dispersal of a given rodent species or population are
417 influenced by different environmental factors, such as mast seeding (Wang et al., 2017), seed
418 size (Yi & Wang, 2015), seed species (in *A. sylvaticus*, Sunyer et al., 2014), predation risk
419 (Leaver, 2004; Sunyer et al., 2013) or pilferage risk (Steele et al., 2008; Samson & Manser,
420 2016). The variability in the patterns of seed management not explained by these environmental
421 factors have been usually interpreted as random ‘noise’ (see Wilson, 1998; Dall et al., 2004).
422 However, part of this apparent noise might be explained by variations in behaviour among
423 individuals documented in our study (see Sih et al., 2004; Sih & Bell, 2008; Dingmanse et al.,
424 2009; Korpela et al., 2011). This fine-scale level, largely overlooked in the ecological
425 framework, would help to increase our understanding on the spatial and temporal variability of
426 the patterns of seed management by seed-dispersing rodents, and may also increase the
427 explanatory power of the ecological models. For example, the fate of seeds in a given seed plot

428 may change depending on the number and identity of the rodents visiting the seed plot.
429 Tracking individuals in field conditions represents, however, a methodological challenge,
430 because scatter-hoarding rodents are usually small, nocturnal and inhabit underground burrows
431 making very difficult to monitor the individual component of behaviour (see Gu et al., 2017;
432 Lichti et al., 2017).

433 We still know little about the nature of the individual variability and potential
434 personalities of scatter-hoarding rodents, so that further studies are needed to undergo on the
435 role of behavioural genetics, physiology and, for example, the consistency of behavioural
436 patterns across generations, or to what extent the environment can influence the potential
437 personalities. Long-term studies carried out in field conditions can shed light on these issues;
438 although in the case of the wood mouse we have found that individuals show a life-span of just
439 a few months in field conditions (Sunyer et al., 2016). On other hand, the ecological
440 consequences of the individual behaviour are also an appealing research field. Our study
441 suggests that the high individual variability of wood mouse in moving seeds can have
442 consequences for seed dispersal in the holm oak (e.g. influencing the variability of acorn
443 dispersal distances and acorn size selection). However, further field studies carried out at wider
444 spatial scales are needed to determine the current role of individual patterns of scatter-hoarding
445 rodents on seed dispersal and plant recruitment.

446

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