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1 **Female mound-building mice prefer males that invest more in building behavior, even when this**  
2 **behavior is not observed**

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8

9 **Abstract**

10 Through behavioral correlations, mate choice could influence the evolution of traits that are not  
11 directly selected for, or even observed. We addressed whether mound building, a unique collective  
12 behavior observed in *Mus spicilegus*, could be favored by female mate choice, irrespective of whether  
13 females were able to observe the behavior. First, we introduced mixed sex groups of wild-born mice in  
14 large terraria with building materials, and assessed male variation in building investment. Second, we  
15 presented females with a choice between males that invested the most versus the least in building.  
16 Females were either able to observe the males during building or not. Third, because overwintering  
17 juveniles rely on mound protection, we hypothesized that building could be a form of paternal care,  
18 and assessed whether males that invested more in building also invested more in direct offspring care.  
19 We showed that females were more attracted to males that invested the most in building, even when  
20 these behaviors were not observed. In addition, direct offspring care was negatively correlated with  
21 males' investment in building, suggesting that two alternative paternal care strategies (mound building  
22 versus direct offspring care) may exist. Our study supports the hypothesis that building could be  
23 detectable by phenotypic cues that differ from building behavior *per se* and that mate choice may  
24 influence the evolution and maintenance of mound building that several authors describe as a common  
25 good.

26

27 **Keywords:** cues, parental investment, preference, personality, sexual selection, cooperation

28

29 **Significance statement**

30 In the mound-building mouse, individuals gather to build a common mound within which juveniles  
31 will spend the winter months. As some males invest more in building than others, we questioned  
32 whether females would prefer males that invest more in building behaviors, even though females  
33 could not observe males' building behaviors before mate choice. We assessed male investment in  
34 building and conducted choice tests. Females were more attracted to males that invested more in  
35 building, even when building was not observed. Hence, building investment seems detectable by  
36 phenotypic cues that differ from building behavior *per se*. Further, the males' investment in building  
37 was negatively correlated with their direct offspring care assessed during retrieval trials. Our findings  
38 indicate that two alternative paternal care strategies may exist in this species, and that mate choice  
39 might influence the evolution of their remarkable collective building.

40

41

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52

53

54 Introduction

55 Behavioral traits often form a suite of correlated traits, so-called behavioral syndromes (Sih et  
56 al. 2004a, b; Réale et al. 2010). For example, aggressiveness is associated positively with exploratory  
57 behavior and boldness in a number of species (Sih et al. 2004a, b; Groothuis and Carere 2005; Boon et  
58 al. 2008; Réale et al. 2009), and negatively associated with parental care (Mutzel et al. 2013). These  
59 behavioral correlations could result from natural and sexual selection that favor particular trait  
60 combinations (Sih et al. 2004a; Réale et al. 2010; Schuett et al. 2010, 2011; Pruitt et al. 2011; Kortet et  
61 al. 2012). Because of such associations, mate choice could indirectly select for a behavioral trait that is  
62 not a mate choice criterion, or even for signals or cues of behaviors that mates did not observe. For  
63 example, by preferring exploratory males, zebra finch females (*Taeniopygia guttata*) simultaneously  
64 select for more aggressive males due to an association between these traits (Schuett et al. 2011). Here  
65 we address whether individuals' investment in a common good could be indirectly selected for by an  
66 association of such behaviors with other sexually selected traits or cues. Such an association would  
67 indicate a potential role of mate preference, and possibly sexual selection, in the evolution of  
68 collective behavior and cooperation (Putland 2001; Tognetti et al. 2012; Van Vugt and Iredale 2013;  
69 Arnocky et al. 2017).

70 Our study model, *Mus spicilegus*, is a socially monogamous mouse, endemic to southeastern  
71 Europe, which possesses a mound-building behavior that is unique among mice (Tong and Hoekstra  
72 2012). After a period of reproduction from spring to late summer, during which each adult breeding  
73 pair produces 4 to 5 litters in individual burrows of simple design (Sokolov et al. 1998), several  
74 individuals gather in late summer to collectively build a common structure in which juveniles born in  
75 late summer and early autumn will overwinter in a nest chamber located under the mound (Muntyanu  
76 1990; Garza et al. 1997; Poteaux et al. 2008; Canady et al. 2009; Tong 2012). Several studies indicate  
77 that juveniles in a given mound may originate from several breeding pairs (up to 4) where the females  
78 are genetically related but the males are unrelated (Garza et al. 1997; Poteaux et al. 2008). In early  
79 spring, these mice leave their mounds, disperse (alone or in small kin groups) and form breeding pairs

80 (Muntyanu 1990; Sokolov et al. 1998; Simeonovska-Nikolova and Gerasimov 2000; Poteaux et al.  
81 2008). In the northern part of the species' range, construction of mounds takes 14-21 days and occurs  
82 from mid-August to mid-November (Muntyanu 1990; Sokolov et al. 1998; Canady et al. 2009). The  
83 mounds are built by the accumulation of plant materials covered with earth and are up to four meters  
84 in diameter and typically 0.5 meters high when freshly built (Muntyanu 1990; Sokolov et al. 1998),  
85 which supports the view that they are built collectively (a single mouse cannot build such a large  
86 structure alone (Szenczi 2012)).

87         The precise age structure of mound builders has yet to be established in natural conditions  
88 (Hölzl et al. 2009; Tong 2012; Tong and Hoekstra 2012). Indeed, direct observations of mound  
89 building in nature are scarce. Furthermore, trapping success can be relatively low during mound  
90 building. For example, observations done during the mound-building period in semi-natural conditions  
91 suggest that, even when they were known to be present, the adults were particularly difficult to trap  
92 (Orsini 1982). Moreover, indirect evidence through trapping around the mounds revealed that adults  
93 could represent 40% to 60% of the population of mice captured from late August to late October  
94 (Simeonovska-Nikolova 2007; Canady et al. 2009; Simeonovska-Nikolova 2012; Tong 2012)  
95 indicating that, although often not detected, adults could be present during the mound construction and  
96 that juveniles could also contribute to building (Sokolov et al. 1998; Canady et al. 2009). From  
97 November, although some adults are still found around the mounds (Canady et al. 2009; Tong 2012),  
98 the population of juveniles increases substantially (Garza et al. 1997; Milishnikov et al. 1998; Canady  
99 et al. 2009; Tong 2012), which could reflect further gathering of mice and/or events of reproduction  
100 during the building season.

101         Altogether, based on the available literature, it seems that the age structure of mound builders  
102 may vary, and that one or several breeding pairs and their juveniles of 3-4 weeks old, or only the  
103 juveniles, may contribute to build the mound. Hence, selection may drive mound building behavior  
104 directly and/or indirectly by increasing survival of juveniles. Here we address whether males that  
105 invest more in mound building are preferred by females.

106           The propensity to build a mound is genetically heritable (Orsini 1982), and investment in  
107 mound building in captivity varies between individuals (Simeonovska-Nikolova and Mehmed 2009;  
108 Serra et al. 2012; Hurtado et al. 2013). Moreover, mound size is highly variable in natural conditions  
109 (Hölzl et al. 2009) and is positively correlated with insulation against water and temperature  
110 fluctuations (Hölzl et al. 2011; Szenczi et al. 2011, 2012). Since small energy savings influence animal  
111 survival even in temperate climate (Vogt and Lynch 1982; Geiser 2004), mound size is thus expected  
112 to influence the probability of offspring survival during the European continental winter (Hölzl et al.  
113 2011; Szenczi et al. 2011, 2012). Hence, it is likely that females would benefit from choosing  
114 hardworking builders as such partners would invest more in mound building and/or transmit their  
115 building ability to their offspring and therefore improve the probability of offspring survival during  
116 winter.

117           However, female mate choice takes place before mound building (for adult builders) or after the  
118 wintering period (for juvenile builders) and, thus, before the potential display of male building  
119 behavior (Muntyanu 1990; Sokolov et al. 1998). Hence, the ability of females to detect male building  
120 behavior through other signals/cues should be positively selected for. Alternatively, females could  
121 indirectly select for male building behavior through their preferences for other traits associated with  
122 males' investment in building. Furthermore, investment in mound building might be seen as a form of  
123 parental care. Behavioral experiments in *Mus spicilegus* revealed that males invest in offspring  
124 attendance, and that highly attendant fathers increase not only their own reproductive success but also  
125 that of their mate (Patris and Baudoin 2000; Feron and Gouat 2007). Parental investment was shown  
126 to be advertised by phenotypic traits in several species (Hill 1991; Östlund and Ahnesjö 1998; Préault  
127 et al. 2005; Hill and McGraw 2006; Gleason and Marler 2010; Bartsch et al. 2015) and could thus  
128 allow females to select good fathers. Hence, a secondary aim of this study was to test whether males  
129 that invest highly in mound building also attend more to their offspring, or if these two forms of  
130 investment are uncoupled.

131           We designed our experiment to test whether females preferred males that varied in their  
132 contribution in mound building when this behavior was observed versus unobserved, and whether

133 male investment in mound building was positively associated with direct paternal care. We assessed  
134 male spontaneous building behavior exhibited during mound construction in captivity by wild mice  
135 captured in agricultural fields in Bulgaria while juveniles. Then, we used two-way choice tests to  
136 assess females' attraction to males that invest more in mound building versus males that invest less.  
137 Finally, we evaluated post-mating paternal care exhibited by males with different investment in  
138 building behavior using pup retrieval experiments: we recorded the number of pups each male  
139 retrieved back to the nest after they were removed from it, and the latency to engage in the retrieving  
140 behavior. We predicted that females would be more attracted to males that invest more versus less in  
141 mound building even when the former did not observe them build. We also predicted that males that  
142 invest more in building would invest more in direct paternal care.

143

## 144 **METHODS**

### 145 *Capture of wild mice*

146 Mound-building mice were captured in northern Bulgaria in September 2011 and were then kept in the  
147 animal facilities of the University of Montpellier in France. We caught the mice in an agricultural area,  
148 at least 2 km away from the village of Rakita (GPS coordinates: 43°16'13.171"N 24°16'16.447"E),  
149 using Sherman live-traps. At this time of year, the mice had already built their mounds. Live-traps  
150 were set around each mound. We weighed and measured all the mice from the nose to the base of their  
151 tail upon capture. A total of 30 males and 28 females, all subadults, captured from 14 mounds were  
152 used in this study. Same-mound mice, irrespective of their sex, were kept in the same laboratory cages  
153 from their capture until the start of the experiments two months later.

154

### 155 *Male investment in mound building*

156 We measured the contribution of each male to mound and nest building in large terraria two  
157 months after capture. This experiment lasted 8 weeks. Earlier studies have shown that even laboratory-

158 born mice of this species would engage in mound building when building material is made available,  
159 suggesting that mound building is a spontaneous behavior (Orsini 1982; Hurtado et al. 2013). Ten  
160 groups of three males and two females were constituted. Sex composition was based on the sex-ratio  
161 observed in the wild during the mound building period (Simeonovska-Nikolova and Gerasimov 2000;  
162 Simeonovska-Nikolova and Mehmed 2009). We placed each group in a large terrarium (1 x 1 x 0.8 m)  
163 containing approximately 0.2 m<sup>3</sup> of earth and stones. The room was maintained at 21/23°C under a  
164 12:12 light/dark cycle (corresponding roughly to the photoperiod observed in the field in  
165 September/October) with lights on at 9.00 pm. Water was available *ad libitum*, and food was provided  
166 on a weekly basis, although daily visits were made to check the well-being of the mice. At the  
167 beginning of each observation session, straw and seeds were provided as building materials in addition  
168 to the earth and stones already present in the terrariums. Both males and females participated in  
169 building. However, we only recorded male behaviors. For each male, five categories of behavior were  
170 recorded: the number of times it dug, carried straw, carried seeds, carried stones, and entered the nest  
171 (Fig. S1). The latter was recorded because the mice were observed entering the nest to build it and  
172 shape it from inside. A single investigator (AT) observed each group during 5 sessions of 1 hour each,  
173 approx. one week apart. Males were ear tagged (7.8 x 2.8 mm, Fine Science Tools GmbH) for  
174 identification. For each terrarium, the number of metallic earrings (1 or 2) and the side of the tag (right  
175 ear, left ear, or both) allowed individual mice to be recognized without having to handle them.

176 We could constitute only five groups of same-mound individuals (three males and two  
177 females). The other five groups included three same-mound males to limit aggression (Sokolov et al.  
178 1998) and two same-mound females from a mound different to that of the males. Unfortunately, for  
179 four out of these five groups, we observed high female mortality (n=8) during the first night in the  
180 enclosure, most likely due to males' aggressiveness. Following this observation, we immediately  
181 removed the two remaining females from the fifth terrarium and placed them in a separate cage.

182 We averaged the data collected during the five observation sessions for each male and for each  
183 of the five behavioral items recorded during building (transport of straw, seeds, and stone, digging and  
184 entering the nest). As highlighted in Fig. S1, mice build a nest as well as a structure closely resembling



185 a mound that had all the characteristics described in the field: i.e. seed storage covered with earth and  
186 plants materials. However, although seed transport and storage did take place (Fig. S1), because 22 out  
187 of 30 mice were not observed transporting seeds, we removed this variable from the analysis. A  
188 principal component analysis (PCA) was applied to the four remaining behavioral items with the aim  
189 of extracting a single factor reflecting male building investment (function *prcomp* in R).

190 At the end of this experiment, all individuals were transferred to laboratory cages, and females  
191 and males of a given group were kept in separate cages to prevent reproduction. They were maintained  
192 in laboratory conditions under a 13.5:10.5 h light/dark cycle (light at 6.30 pm), corresponding to the  
193 photoperiod during the breeding season (early spring). Food and water were available *ad libitum*, and  
194 cotton was provided as nesting material. They were kept in these conditions until the beginning of the  
195 next experiment.

196

#### 197 *Female attraction*

198 We measured female attraction to males in a Y maze following the procedure described in Smadja and  
199 Ganem (2002) six months after their capture. The stimuli were composed of 5 pairs of males. Males of  
200 each pair shared the same terrarium during the mound-building experiment and belonged to one of the  
201 five terraria in which females were present. In each of these terraria, we selected among the three  
202 males the male that invested the most and the male that invested the least in order to present to the  
203 females a choice between contrasting levels of building behavior. To that aim, we used the PCA factor  
204 reflecting the most male investment in building (see Results).

205 Each female was tested once. We tested female attraction to males that invested the most  
206 versus the least in building when building was observed (females that shared an enclosure with 3  
207 males during mound building were presented with a choice between the male that invested in building  
208 the most or the least in the triad) (n=10 females), and when building was unobserved (females that did  
209 not share an enclosure with males were given the choice between a pair of males composed of the  
210 males that invested the most and the least from a triad randomly chosen) (n=10 females).

211 A single investigator (AT) conducted all the tests. All mice were more than 6 months old and  
212 sexually mature. To maximize the expression of sexual attraction, females were tested while sexually  
213 receptive (i.e., estrus or proestrus/estrus, assessed with vaginal smears).

214 The Y maze was transparent (plexiglas and plastic ware) and composed of a main branch (5  
215 cm diameter, 35 cm long) connected to two secondary branches (5 cm diameter, 25 cm long). Boxes  
216 (35 x 23 x 13 cm) with transparent perforated doors were connected at the end of each branch (for an  
217 illustration of the apparatus see: Smadja and Ganem 2002). One week before the experiment, each  
218 female was allowed to explore the empty Y maze for 15 minutes in order to become habituated.

219 At the start of each test, a female was placed in a box connected to the main branch of the  
220 apparatus. The two stimuli were randomly assigned to one or the other peripheral boxes (the identities  
221 of the stimuli was not known by the observer). We then opened the door of the female's box and  
222 started to record its behavior when the female crossed the box door. In all tests, the females entered  
223 both secondary branches of the Y maze. During the 10-minute observation, we recorded the time spent  
224 by females: i) in each secondary branch (including when females were in contact with the perforated  
225 door but when the male was not behind the door), and ii) interacting with the male, or sniffing or  
226 licking the transparent perforated door when the male was just behind the door. This is a classical  
227 method to measure female preference (e.g. Smadja and Ganem 2005; Latour et al. 2013) that was  
228 shown to constitute a good proxy of female propensity to engage in mating with the preferred male  
229 (Patris and Baudoin 1998; Smadja and Ganem 2002). We implemented General Linear Mixed Models  
230 to test whether male attraction was influenced by their investment in building. For this purpose, we  
231 used GLMMs with a quasi-binomial error structure (*glmmPQL* function of the *MASS* package in R) in  
232 which we included the identity of each pair of males as a random effect. In the first model, the  
233 response variable was the proportion of time spent by the female in the left versus right side of the  
234 maze. In a second model, it was the proportion of time the female was in close contact with the male  
235 of the left versus right side of the maze. In both models, we included two explanatory variables: (i) a  
236 binary variable concerning male investment in building (1 if the male on the left was the one that  
237 invested the most in building behaviors, 0 if it was the male that invested the least) and (ii) a binary

238 variable reflecting the treatment (1 if the female observed male building behaviors, 0 if not). We also  
239 tested the interaction between these two variables to test whether observing male building influenced  
240 female preferences. When the interaction was not significant, we removed it from the model.

241           At the end of the experiment, all individuals were returned to their home cage and maintained  
242 under laboratory conditions until the next experiment.

243

#### 244 *Direct paternal care*

245 We used a pup retrieval procedure, a test used commonly to measure parental care in rodents (Dudley  
246 1974; Cohen-Salmon et al. 1985), including *Mus spicilegus* (Patris and Baudoin 2000). We first  
247 randomly paired females (n=20) and ‘unfamiliar’ males (i.e., captured in different mounds in the  
248 field). During the first week, the two members of the pair were maintained in the same cage but  
249 separated with a wire net so that they could first become familiar with each other. We maintained them  
250 in laboratory conditions under a 13.5:10.5 light/dark cycle (light at 6.30 pm), corresponding to the  
251 photoperiod of the breeding season in the field. Food and water were available *ad libitum*, and cotton  
252 was provided as nesting material. Ten of the 20 pairs successfully bred (a low breeding rate is often  
253 observed for wild-born mice kept under laboratory conditions, GG pers. obs.) and could hence  
254 participate in this experiment that began 18 months after capture. Litter size varied from 5 to 12 pups.

255           On the day of birth, we placed the mice in a large terrarium (70 x 30 x 30 cm). The terrarium  
256 contained clean sawdust, food and water. One corner also contained cotton and cardboard rolls as nest-  
257 building material.

258           All males were tested twice: approximately four days (mean  $\pm$  SD:  $3.7 \pm 0.8$  days) and six  
259 days ( $6.3 \pm 0.9$  days) after the birth of their first litter. During these two sessions, we first removed the  
260 breeding pair from the terrarium. We then removed three of the pups from the nest and placed them at  
261 the opposite end of the terrarium. We isolated these three pups from their littermates and the nest by  
262 placing a transparent plastic separation in the middle of the terrarium. The male was then put back in

263 the side of the terrarium containing the nest. After 30 seconds, we removed the plastic separation and  
264 we measured (i) male latency before the start of retrieval of the isolated pups, and (ii) the number of  
265 pups retrieved to the nest during the next fifteen minutes. Both of these measures were averaged over  
266 the two test sessions, and we used Spearman correlation tests (two-tailed tests, function *cor.test* in R)  
267 to assess their potential association with the male building score measured during the mound-building  
268 experiment (first experiment above). For males that did not retrieve any pups, the male latency to  
269 retrieve was set at 15 minutes (i.e., the duration of the experiment). Because the Spearman correlation  
270 test relies on ranks, this choice did not influence the results.

271 Because this species is nocturnal and particularly active during the first few dark hours  
272 (Simeonovska-Nikolova and Mehmed 2009), all observations (mound building, female preferences,  
273 and paternal investment) were conducted one to two hours after the beginning of the dark period under  
274 dim red light. To minimize observer bias, we used blind methods when behavioral data were recorded  
275 (preferences tests and retrieval experiments). We recorded all observations using the Observer  
276 software Version 5 (Noldus Information Technology). All statistical analyses were performed using  
277 the R software, version 3.4.2 (R Core Team 2017).

278

## 279 **RESULTS**

### 280 *Male investment in building*

281 In total, during the 50 hours of observation, each male transported 0 to 70 pieces of straw (mean  $\pm$  SD:  
282  $18.1 \pm 19.4$ ), and 1 to 99 ( $20.9 \pm 23.9$ ) stones (approximately  $1 \text{ cm}^3$  in size). The frequency of digging  
283 varied between 0 and 35 times ( $10.1 \pm 8.9$ ), and they entered their nest 2 to 35 times ( $12.6 \pm 9.9$ ). We  
284 used a PCA to extract a single factor reflecting male global investment in mound building and  
285 avoiding giving too much weight to a specific behavior. The first two axes of the PCA, including the  
286 four building items, captured 80% (45% and 34% respectively) of the total variation. The first axis  
287 was positively correlated with the number of times a male entered the nest ( $r = 0.42$ ), negatively  
288 correlated with stones transport ( $r = -0.66$ ) and digging frequency ( $r = -0.62$ ), and not correlated with

289 straw transport ( $r = 0.06$ ). We hence considered that this axis could represent a measure of  
290 specialization in building tasks (Serra et al. 2012; Hurtado et al. 2013) rather than a measure of global  
291 investment. The second axis was positively correlated with all four variables: frequency of digging ( $r$   
292  $= 0.28$ ), number of stones ( $r = 0.17$ ) and straw transported ( $r = 0.76$ ), and number of entrances into the  
293 nest ( $r = 0.57$ ), and we considered that it could reflect male global investment in building and hence a  
294 pertinent measure allowing to identify males that invested the most and the least in building behaviors.

295 Investment in building was not related to male weight ( $10.26 \pm 0.87$  grams) or size ( $7.14 \pm 0.34$   
296 cm) at capture (Spearman correlation test: weight:  $\rho = 0.11$ ,  $p = 0.58$ , size:  $\rho = 0.01$ ,  $p = 0.95$ ) nor to  
297 their weight ( $11.64 \pm 1.6$  grams) at the end of the building experiment ( $\rho = 0.13$ ,  $p = 0.53$ ). Moreover,  
298 we did not detect any difference in individual building when comparing males belonging to mixed  
299 groups (containing females) to males belonging to all-male groups (Wilcoxon rank sum test:  $W = 86$ ,  
300  $p = 0.43$ ).

301

### 302 *Female attraction*

303 We found no effect of the interaction between male investment in building and treatment in any  
304 model, suggesting that observing male building behaviors did not influence female attraction  
305 (glmmPQL with time spent by females ( $n=20$ ) in the branches as response variable:  $t=1.00$ ,  $P=0.92$ ;  
306 glmmPQL with time spent by females ( $n=15$ ) in close proximity to the males as response variable:  $t=-$   
307  $1.03$ ,  $P=0.34$ ).

308 Male investment in building did not influence the proportion of time females ( $n=20$ ) spent  
309 exploring the two branches (52% of time was spent on the side of the male that invested the most  
310 versus the least; glmmPQL:  $t=1.30$ ,  $P=0.21$ ; Table S1; Fig. 1). However, it did significantly influence  
311 the proportion of time females ( $n=15$ ) spent in proximity to the males (75% of time was spent close to  
312 the male that invested the most versus the least; glmmPQL:  $t=3.69$ ,  $P=0.006$ ; Table S2; Fig. 1):  
313 females spent more time in close proximity to the male that invested the most in building behaviors  
314 compared to the time spent with the male that invested the least (median [1<sup>st</sup> quartile; 3<sup>rd</sup> quartile] of

315 the difference of time spent with the male that invested the most versus the least in building  
316 behaviors=8.4 [4.6; 11.7] s).

317

### 318 *Investment in mound building & direct paternal care*

319 The males (n = 10) retrieved 0 to 3 pups at each session (median [1<sup>st</sup> quartile; 3<sup>rd</sup> quartile]: 1.5 [0; 3]  
320 for the first session; 2.5 [0.25; 3] for the second session). For each male, the number of pups retrieved  
321 during the first versus the second session was not significantly different (paired Wilcoxon rank test: 0  
322 [-0.75; 0] pups,  $V = 5.5$ ,  $p = 0.68$ ). For sessions in which at least one pup was retrieved (n=12), the  
323 latency to retrieve the first pup was between 23 and 810 seconds (171 [36; 325] s).

324 Direct paternal care was negatively associated with male investment in building: across the 20  
325 sessions, the males that invested more in building retrieved fewer pups back to the nest (Spearman  
326 correlation test: n=10 males,  $\rho = -0.67$ ,  $p = 0.04$ ; Fig. 2a) and presented a higher latency to retrieve the  
327 first pup (n=10 males,  $\rho = 0.71$ ,  $p = 0.02$ ; Fig. 2b).

328

### 329 **Discussion:**

330 Mate choice and sexual selection could favor the evolution of traits that are not directly selected for  
331 (Schuett et al. 2010, 2011). Here we addressed whether mound building, a spontaneous behavior  
332 observed both in wild- and laboratory-born individuals of *Mus spicilegus*, could be favored during  
333 female mate choice even though females were not able to observe the building activity of males.  
334 Indeed, the presence of adults and juveniles around mounds during the building period suggests that  
335 the two cohorts (adults and juveniles when 3-4 weeks old) could be involved in building  
336 (Simeonovska-Nikolova 2007, 2012; Canady et al. 2009; Tong 2012), further indicating that mate  
337 choice would take place before mound building (for the adults) or after (for the juveniles) and involve  
338 unfamiliar partners (Garza et al. 1997). Aiming to get insight into the mechanisms favoring building  
339 behavior, we asked whether female mate choice could favor males that invest more versus less in

340 mound building behaviors and whether males that invest more are also more involved in direct  
341 parental care using pup-retrieval experiments.

342 Our findings indicate that females were more attracted to males that invested more in building  
343 behaviors over males that invested less, even when building behaviors were not observed. This  
344 suggests that female attraction to males could be influenced by cues that are different from building  
345 behaviors *per se*, or by attraction to traits associated with male investment in building. We also show  
346 that direct parental care is negatively correlated with male investment in mound building, suggesting a  
347 trade-off between these two behaviors.

348 Our findings raise the question of which signals or cues females are responding to when they  
349 show an attraction to males that invest more in mound building. In our experiment, females were more  
350 attracted to males that invested more versus less in building, even without having observed them build.  
351 Hence, phenotypic cues advertising male investment in building may exist in this species. Such cues  
352 could be based on acoustic, olfactory, or visual traits, since all of them are involved in mice  
353 communication (e.g.: Hurst and Beynon 2004; Musolf et al. 2010) and were available to females in  
354 our test apparatus. Their detection by females could influence their sexual preferences, as some sexual  
355 pheromones do in several species, including mice (Roberts et al. 2010; Li and Liberles 2015). An  
356 alternative explanation could also be that female attraction to males that invest more in building was  
357 not directed to building *per se* but to other traits with which investment in building is associated. We  
358 did not observe any link between male size or weight and investment in building, suggesting that male  
359 condition is unlikely to be one of these traits. Interestingly, experimental studies in the mound-  
360 building mouse found that agonistic behaviors between unfamiliar males and females are positively  
361 linked with sexual motivation (Busquet et al. 2009; Simeonovska-Nikolova and Lomlieva 2012).  
362 Because of the expected high cost of mound building and its important role in the success of  
363 overwintering, individuals that invest more in mound building are likely to more aggressively protect  
364 resources and defend their mound from intruders. We can therefore speculate that male aggressiveness  
365 or dominance might be sexually selected traits associated with building, leading to the indirect  
366 selection of building behavior through female mate choice. During our preference tests, we did not

367 observe agonistic behaviors between males and females through the perforated doors; furthermore,  
368 males that invested more in mound building were not observed to try to attract more female attention  
369 than males that invested less. However, chemosensory cues of dominance and aggressiveness are  
370 present in the urine and preputial glands of male mice and therefore could have been detected by  
371 females during their interactions with the males (Harvey et al. 1989; Hurst and Beynon 2004; Soini et  
372 al. 2009; Mucignat-Caretta and Caretta 2014). Follow-up studies should thus investigate which traits  
373 are used by female *Mus spicilegus* during mate choice that are associated with building behavior. Such  
374 studies may particularly focus on dominance, aggressiveness and other personality traits.

375         In *Mus spicilegus*, the inclination of females to prefer males that invest more in mound  
376 building could be an adaptive strategy. Choosing a male that invests highly in building could increase  
377 females' fitness in several ways. First, since mound size is positively correlated with water-insulation  
378 and soil temperature inside the mound (Hözl et al. 2011; Szenczi et al. 2011, 2012), choosing a male  
379 that invests more energy and time in mound building could increase offspring survival during the  
380 winter. Second, mound-building behavior seems to be genetically heritable (Orsini 1982). If the level  
381 of investment in building was also heritable, by choosing a male that invests more in building, females  
382 could improve the ability of their offspring to build a mound, and hence increase the chance of  
383 survival of their own progeny. Third, given the attractiveness of the males that invest more in building  
384 behaviors, females could also increase their sons' reproductive success (sexy son hypothesis:  
385 Weatherhead and Robertson 1979).

386         Interestingly, we found a negative correlation between direct paternal care and building  
387 investment. Previous experimental studies involving the mound-building mouse found intense paternal  
388 investment, such as covering and warming the pups (Patris and Baudoin 2000), and males that  
389 exhibited the highest levels of offspring attendance increased their reproductive success by reducing  
390 their mate's inter-litter intervals (Feron and Gouat 2007). As both parental investment and building are  
391 likely to be energetically costly, the negative association observed between them may indicate the  
392 existence of a tradeoff. In addition, since parents are likely to build a mound for their offspring, mound  
393 building may be considered a form of parental care (as defined by (Royle et al. 2012)). In this case,



394 this negative association might suggest the existence of two alternative parental care strategies. Hence,  
395 an interpretation of our results could be that different behavioral traits may correspond to different  
396 types of fathers with regard to how they take care of offspring. Such alternative strategies in offspring  
397 care were previously observed in some cooperative breeding species, such as cichlids,  
398 *Neolamprologus pulcher*, or the noisy miner, *Manorina melanocephala*, in which different types of  
399 helpers seem to exist (Arnold et al. 2005; Bergmüller and Taborsky 2007), but to our knowledge, they  
400 were not extensively studied in relation to parental care.

401 Cooperative behavior is defined as a behavior that benefits others while reducing the relative  
402 fitness of the performer of that behavior and hence could be selected against (West et al. 2007).  
403 Mound building possesses *a priori* those characteristics and we propose that it may be considered as a  
404 cooperative behavior, favored by female mate choice as observed in humans (Farrelly et al. 2007;  
405 Tognetti et al. 2014, 2016; Arnocky et al. 2017) and some cooperatively breeding birds (Reyer 1984;  
406 Jones 1998; Doutrelant and Covas 2007).

407 A limitation of our study concerns the small sample sizes, due to restrictions on field captures,  
408 and unexpected mortality events. Nevertheless, male investment in building significantly influenced  
409 female attraction and this result is particularly promising for more extensive research.

410 In conclusion, our results raise questions about the mechanisms involved in the evolution of  
411 mound building and provide support to the hypothesis that such behavior could be detectable by  
412 phenotypic cues different from building *per se*. While the mechanisms enabling females to prefer the  
413 males that invest the most in building behaviors in this species are still unknown, our results suggest  
414 that mate choice might influence the evolution and maintenance of mound building. Last but not least,  
415 several authors pointed out the collaborative aspect of mound building, and some evidence indicates  
416 that several breeding pairs and their offspring could be involved in building this common good. Future  
417 studies should test whether building could be considered a cooperative behavior and whether sexual  
418 selection is another pathway by which cooperative building in this species might evolve.

419

420 **Compliance with Ethical Standards**

421 *Ethical Approval*

422 Mouse sampling was performed with the authorization of the Bulgarian Ministry of the Environment  
423 and Water (permit N°33-00-140). The study complied with all the relevant laws of France and mice  
424 handling and behavioral tests were authorised by the French authorities (Direction Départementale de  
425 la Protection des Populations de l'Hérault – Ministère de l'Agriculture, permit N°C34-265). This study  
426 also followed the ABS/ASAB guidelines for the ethical treatment of animals. We were particularly  
427 committed to limiting the number of mice trapped and tested, and mice were provided an enriched  
428 environment and diversified food to reduce their stress as much as possible.

429 *Conflict of Interest*

430 The authors declare that they have no conflict of interest.

431 *Data availability*

432 The datasets analysed during the current study are available in the figshare repository,  
433 <https://doi.org/10.6084/m9.figshare.5562664>

434

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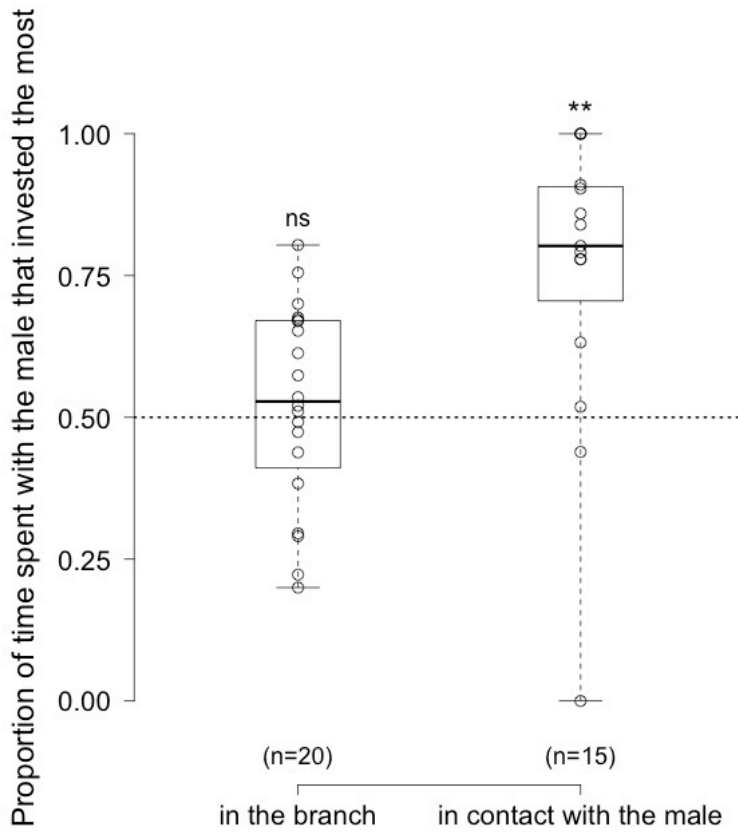
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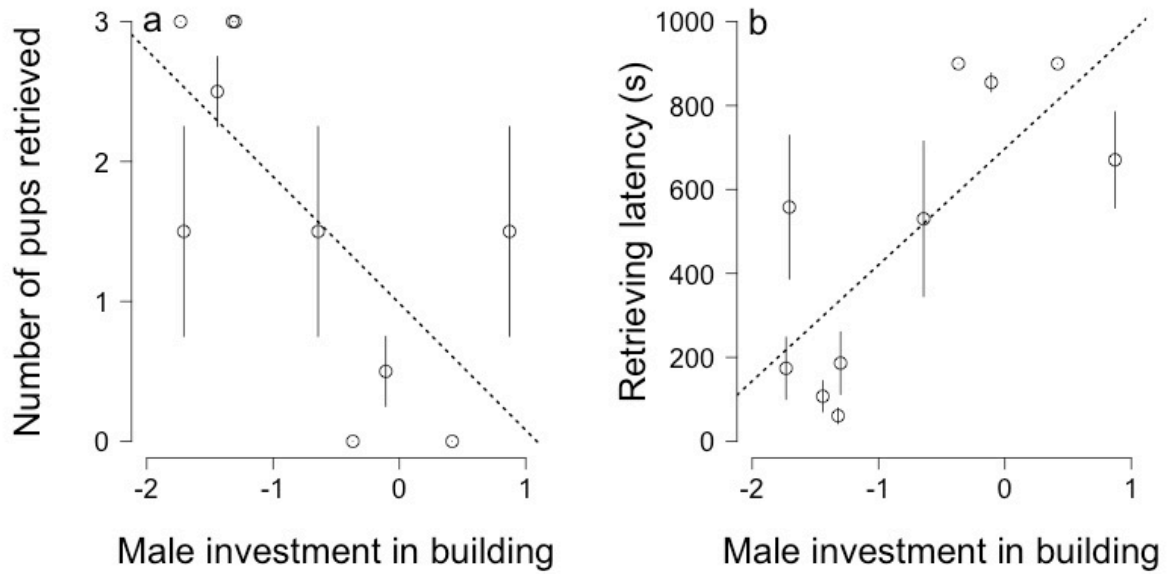
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592

593 **Fig. 1**

594 Box plot representation of the proportion of time females spent exploring the branch of, or in  
595 proximity to the male most involved in building, relative to the total time spent exploring the two  
596 branches or in close proximity to the two males. The horizontal dotted line corresponds to a random  
597 choice. A value over 0.50 indicates preference for the male that invests the most in mound building.  
598 Medians (thick lines), first and third quartiles, whiskers representing the entire data range and  
599 individual data points are indicated. ns: non-significant, \*\* p<0.01



600

601 **Fig. 2**

602 Relationship between male investment in building and paternal care, measured as the average number  
 603 of pups retrieved to the nest (a), and as the latency to retrieve the first pup to the nest (b). Error bars  
 604 represent the standard error of the mean. Spearman correlation tests indicate that males investing more  
 605 in mound building retrieved fewer pups back to the nest and presented a higher latency to retrieve the  
 606 first pup.

607



608 Supplementary data: Tables S1 & S2.

609

610 **Table S1. Influence of male investment in building and treatment (observed building by the**  
611 **female versus not) on the proportion of time females spent exploring the left versus right side of**  
612 **the maze (n= 20).** We used a Generalized linear mixed model fitted by penalized quasi-likelihood  
613 (glmmPQL, binomial error), with male pair's identity as a random effect. We included two  
614 explanatory variables: a binary variable concerning male investment in building (1 if the male on the  
615 left was the one that invested the most in building behaviors, 0 if it was the male that invested the  
616 least) and a binary variable reflecting the treatment (1 if the female observed male building behaviors,  
617 0 if not). The initial model also considered the interaction between male investment in building and  
618 treatment, but it was excluded during model simplification due to its non-significance.

619

620

<b>Predictor variables</b>	<b>Estimate</b>	<b>S.E.</b>	<b>df</b>	<b>t</b>	<b>P</b>
Intercept	-0.16	0.31	13	-0.52	0.61
Male investment in building	0.51	0.39	13	1.30	0.21
Treatment	-0.37	0.38	13	-0.97	0.35

621

622

623

624

625 **Table S2. Influence of male investment in building and treatment on the proportion of time the**  
626 **female spent in contact with the male of the left versus right side of the maze (n= 15).** We used a  
627 Generalized linear mixed model fitted by penalized quasi-likelihood (glmmPQL, binomial error), with  
628 male pair's identity as a random effect. We included two explanatory variables: a binary variable  
629 concerning male investment in building (1 if the male on the left was the one that invested the most in  
630 building behaviors, 0 if it was the male that invested the least) and a binary variable reflecting the  
631 treatment (1 if the female observed male building behaviors, 0 if not). The initial model also  
632 considered the interaction between male investment in building and treatment, but it was excluded  
633 during model simplification due to its non-significance.

634

635

<b>Predictor variables</b>	<b>Estimate</b>	<b>S.E.</b>	<b>df</b>	<b>t</b>	<b>P</b>
Intercept	-1.16	0.59	8	-1.96	0.09
Male investment in building	2.51	0.68	8	3.69	0.006
Treatment	-0.16	0.70	8	-0.23	0.83

636

637

Figure S1: Photographs of mounds built in captivity

At the beginning of the experiment, the soil of each terrarium was uniformly covered with earth and stones. Additional material (straw and seeds) were added weekly at the center of each terrarium.

All mice built a nest made of straw in a corner of the terrarium (A), and constructed a 'mound like' stucture made of stone and straw (B). Under some parts of the 'mound like' structures we observed the presence of seeds indicating seeds transport, gathering and storage (C). Tunnels were also observed (D).

A

B

C

D

