

1     **Sexual selection and the evolution of male and**  
2             **female cognition: a test using experimental**  
3             **evolution in seed beetles**

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17

## 18 **Abstract**

19 “The mating mind hypothesis”, originally aimed at explaining human cognition, holds that  
20 the socio-sexual environment shapes cognitive abilities among animals. Similarly, general  
21 sexual selection theory predicts that mate competition should benefit individuals carrying  
22 “good genes” with beneficial pleiotropic effects on general cognitive ability. However, few  
23 experimental studies have evaluated these related hypotheses due to difficulties of performing  
24 direct tests in most taxa. Here we harnessed the empirical potential of the seed beetle study  
25 system to investigate the role of sexual selection and mating system in the evolution of  
26 cognition. We evolved replicate lines of beetle under enforced monogamy (eliminating sexual  
27 selection) or polygamy for 35 generations and then challenged them to locate and  
28 discriminate among mating partners (male assays) or host seeds (female assays). To assess  
29 learning, the same beetles performed the task in three consecutive rounds. All lines learned  
30 the task, improving both within and between trials. Moreover, polygamous males  
31 outperformed monogamous males. However, there were no differences in the rate of learning  
32 between males of the two regimes, and polygamous females showed no improvement in host  
33 search, and even signs of reduced learning. Hence, while sexual selection was a potent factor  
34 that increased cognitive performance in mate search, it did not lead to the general increase in  
35 cognitive abilities expected under the “mating mind” hypothesis or general “good genes”  
36 theory. Our results highlight sexually antagonistic (balancing) selection as a potential force  
37 maintaining genetic variation in cognitive traits.

## 38 **Background**

39 Cognitive traits allow for behavioural plasticity which can fundamentally change  
40 evolutionary dynamics and the mode of, and limits to, adaptation<sup>1-4</sup>. Cognitive abilities also  
41 vary widely among animal taxa and there are many hypotheses aimed at explaining this  
42 interspecific variation. Most evolutionary explanations typically emphasize the importance of  
43 trade-offs and species ecology in shaping cognition<sup>5-10</sup>. One such hypothesis is the idea that  
44 the social system of a species is particularly important in shaping cognitive abilities<sup>11</sup>. Indeed,  
45 the complex social structure of human societies has been suggested as a main driver of our  
46 species' intelligence<sup>12</sup>. This idea has also been expanded and popularized to include the  
47 socio-sexual environment, advocating the view that sexual selection and competition over  
48 mating partners has been an important factor contributing to human cognition, which only  
49 later allowed the successful colonization of new environments and unprecedented cultural  
50 innovations of our species ("*The mating mind hypothesis*")<sup>13,14</sup>.

51

52 The arena for socio-sexual interactions and associated cognitive decision making appear  
53 somewhat different in humans compared to other animals. However, it is perhaps only from  
54 an anthropocentric perspective that these differences can be seen as larger than those between  
55 any other two animals with different mating systems<sup>15</sup>, suggesting that the mating mind  
56 hypothesis could be generalized to explain variation among non-human taxa<sup>16</sup>. Indeed, the  
57 idea that sexual selection requires cognitive abilities has been widely explored (e.g. <sup>5,14,16-18</sup>).  
58 However, comparative evidence for a direct link between mating system variation and animal  
59 cognition is mixed<sup>16,17,19</sup>. For example, in primates monogamy rather than polygamy is  
60 associated with larger brain size<sup>20</sup>, providing evidence against the hypothesis that sexual  
61 selection leads to increased cognition but not excluding that complex social structure is  
62 important, given that maintaining monogamous pair-bonds may be cognitively demanding<sup>5,11</sup>.

63 In both primates<sup>6</sup> and birds<sup>21</sup>, environmental complexity is more strongly associated with  
64 brain size than the social system of the species. Moreover, in bats, males of species where  
65 females are promiscuous tend to have smaller brains but larger testes compared to species  
66 where females exhibit mate fidelity<sup>22</sup>, suggesting that sexual selection may even lead to  
67 decreased cognitive ability via trade-offs with expensive secondary sexual traits.

68

69 These comparative studies provide a less than convincing case for an important role of the  
70 mating system in the evolution of cognition. Given the many, potentially confounding,  
71 factors associated with animal sociality, mating systems and ecology, it may be that  
72 controlled experiments are needed to compliment comparative methods<sup>23</sup> and evaluate the  
73 generality of the mating mind hypothesis as applied to animals in general. The question thus  
74 remains whether sexual selection and mating system variation generally are important for the  
75 evolution of cognition in its widest definition – i.e. does selection for cognitive performance  
76 during mating competition lead to greater cognition when applied to other tasks or behaviors?

77

78 The mating mind hypothesis is rooted in general sexual selection theory<sup>17,24</sup>, which holds that  
79 competition over access to mating partners should select for males that carry genomes free of  
80 deleterious mutations (i.e. males carrying the “good genes”)<sup>25</sup>. Since most new mutations are  
81 thought to be deleterious and have wide ranging pleiotropic effects on fitness related traits<sup>26</sup>,  
82 it follows that males that are successful in mating competition should on average be superior  
83 performers, and pass on these “good genes” to both sons and daughters<sup>27</sup>. Hence, the mating  
84 mind and good genes hypothesis make largely parallel predictions of an association between  
85 the mating system and general cognitive ability.

86

87 Here we tested the role of sexual selection and mating system variation in the evolution of  
88 cognition by harnessing the empirical potential of experimental evolution and the seed beetle  
89 study system. We evolved replicate evolution lines of *Callosobruchus maculatus* beetles  
90 under enforced monogamy (excluding sexual selection) or natural polygamy (including high  
91 levels of sexual competition and mate choice) for 35 generations. We then subjected these  
92 lines to a cognitively challenging spatial and chemo-sensory task, composed of mate finding  
93 and discrimination in males, and host seed finding and discrimination in females. We also  
94 assessed cognitive learning for both tasks (in males and females respectively) by letting the  
95 same beetles perform the task in three consecutive rounds with interspaced acclimation  
96 periods. Hence, our design allowed us to assess whether experimental evolution had led to  
97 improved cognitive performance in the specific task (male mate search and discrimination)  
98 known to be under differential selection in the monogamy and polygamy regime, and then to  
99 explore whether evolution under the contrasting mating systems had led to genetic changes in  
100 general cognitive ability inferred from i) improved female host search and discrimination,  
101 and ii) improved cognitive learning in the tasks, assessed in respective sex.

102

## 103 **Methods**

### 104 *Study species*

105 *C. maculatus* seed beetles are common pests of legumes (Fabaceae) in Africa and Asia.  
106 Females lay eggs on seeds and larvae burrow into the seed where the entire development  
107 occurs<sup>28</sup>. Beetles emerging from seeds are reproductively mature and require neither water  
108 nor food to reproduce (e.g.<sup>28,29</sup>). Adults typically die in 7-14 days after emergence in the  
109 absence of food or water (e.g.<sup>30</sup>).

110

111 Sexual selection is intense in this species, including both pre- and post-copulatory  
112 processes<sup>31-36</sup>. Sexual selection is thus likely to put demands on both male and female  
113 cognitive abilities associated with mate choice, including assessing sex, age, body size,  
114 phenotypic quality, as well as mating status of potential mating partners, as all these choices  
115 can potentially influence reproductive success<sup>28,31,37-39</sup>. In the lab environment males search  
116 for females among beans, putting additional demands on male spatial orientation and use of  
117 olfactory cues to locate and discriminate females<sup>40</sup>, who when mated often hide amongst the  
118 beans to escape costly re-mating attempts by males<sup>34-36</sup>.

119

120 Female host plant search and discrimination is complex. *C. maculatus* has a wide repertoire  
121 of fabaceous host plants<sup>41</sup> but females have a clear host hierarchy and preference, and they  
122 discriminate between high quality and low quality species (e.g. <sup>42,43</sup>). In the lab environment  
123 females are typically presented with beans from one host species, but need to discriminate  
124 among good and bad quality seeds as well as against egg-laden seeds, as high larval density  
125 or poor quality host seeds limit both survival and size at maturity of offspring, and thus come  
126 at substantial fitness costs<sup>38,43</sup>.

127

128 The experimental evolution lines (see below) come from a genetic stock recently isolated  
129 from the wild<sup>44</sup>. *C. maculatus* utilizes both natural habitats, where host plant patches used for  
130 both egg laying and adult nectar feeding are more widely distributed, as well as grain  
131 storages, where adult food is absent but egg laying substrate and population density is  
132 higher<sup>38,41,43</sup>. Thus, selection on spatial cognition and chemosensory cues is likely always  
133 strong in natural populations, but may take different forms, which is predicted to maintain  
134 genetic variation in the cognitive traits under study, as seen for other characters related to  
135 these alternative environments (e.g. <sup>45</sup>).

136

137 ***Polygamous and Monogamous experimental evolution lines***

138 The lines used in this study are thoroughly described in Martinossi-Allibert et al.<sup>46</sup>. In brief,  
139 the lines and the outbred base population from which they originate were maintained under  
140 controlled temperature (29°C), humidity (50%RH) and light cycle (12L: 12D), and reared on  
141 the preferred host plant<sup>41</sup> *Vigna unguiculata* (black-eyed bean). We used six lines in this  
142 study; three replicate lines evolving under enforced monogamy (removing sexual selection),  
143 and three lines evolving under polygamy in the natural lab environment which applies sexual  
144 selection by allowing pre- and post-copulatory mate competition and choice, in addition to  
145 the fecundity and viability selection acting in the monogamy regime. There are two more  
146 lines in the study by Martinossi-Allibert et al. from a third evolution regime which applied  
147 sexual selection on males while excluding selection on adult females all together. However,  
148 since our hypotheses were most straightforward to test by comparing the effect of adding  
149 sexual selection (polygamy regime) to an already natural socio-sexual mating system  
150 (monogamy regime), we did not include these two lines in this study.

151

152 Effective population size in each regime was kept approximately equal ( $N_e = 150$ ,  $N_{\text{monogamy}} =$   
153  $246$ ,  $N_{\text{polygamy}} = 300$ ) and the number of beans provided as egg laying substrate in each  
154 regime was standardized to give the same, relatively low, juvenile density (2-4 eggs/bean) to  
155 minimize (and equalize) larval competition<sup>46</sup>. The polygamy and monogamy regime show  
156 differences in line with good genes effects of sexual selection: already following 16-20  
157 generations of experimental evolution, polygamy lines showed higher lifetime reproductive  
158 success as well as population fitness compared to monogamy lines<sup>46</sup>.

159

160 *Cognitive performance of males in the mate searching task*

161 We measured focal males' (i.e. derived from one of the evolution lines) ability to localise and  
162 discriminate females in a spatially complex arena made up by a petri dish measuring 150 mm  
163 in diameter containing reference beetles of both sexes (Fig. 1). The reference beetles  
164 originated from the original base population from which the selection lines were derived.  
165 Virgin reference beetles, 0-24h old, were frozen at -20°C and defrosted just previous to a trail  
166 and glued to the arena (with their ventral side facing downwards), making sure that the focal  
167 beetles did not shift their position during the three consecutive behavioural trails. The same  
168 reference beetles were used for the full run of three trails before being replaced by new  
169 beetles.

170

171 The arena floor was covered with paper (Fig. S1) designed to aid spatial memory and  
172 learning. The paper had pale red background and a white large circle connected to a white  
173 channel leading away from it towards the inner wall of the opposite side of the arena, ending  
174 in a smaller circle at which the four focal males were placed at the initiation of each trial (see  
175 below). Each large white circle contained four equidistant points where the freshly defrosted  
176 reference females were glued. The 'channel' was connected to the circle to easier allow focal  
177 males to learn and find the location of females. The remaining pale red background  
178 comprised ten equidistant points where the freshly defrosted reference males were glued (Fig.  
179 1). A second type of arena with inversed color scheme was used to control for effects of  
180 potential color preferences in the beetles (Fig. S1).

181

182 The assays were run on a heating plate set at 30°C, with six arenas on the plate scored  
183 simultaneously. In each arena, 4 focal males were introduced simultaneously. This was for  
184 two reasons, i) to increase activity, because beetles become more active in group, and ii) to



185 efficiently score as many beetles as possible. Assays were initiated by consecutively  
186 introducing the four beetles into the small circle in each of the 6 replicate arenas. This took  
187 ca. 60 seconds after which behavioral observations were taken in the same sequential order  
188 each minute for the subsequent 10 minutes. Each census time of an arena lasted for 10  
189 seconds before the next arena in line was observed. During the 10 seconds we recorded  
190 whether each of the four beetles in the arena were in contact with a reference individual and  
191 whether this was a male or a female. This contact usually meant that males were trying to, or  
192 even “successfully” mated with both (dead) males and females (males try to mate readily  
193 with other males in this species and population<sup>40</sup>). The four beetles were thus scored as a  
194 group and could at each census time get a score between 0 and 4 for mating attempts on  
195 reference males and females.

196

197 Our measurements are likely to capture two independent aspects of seed beetle cognition; i)  
198 the ability to locate and remember the location of reference individuals in a spatially complex  
199 two-dimensional landscape, and ii) via chemo-sensory cues discriminate the sex of the  
200 located reference individual (which seems cognitively demanding in seed beetles:<sup>40</sup>, as in  
201 many other insects<sup>47</sup>).

202

### 203 ***Cognitive performance of females in the host searching task***

204 We measured focal females’ ability to find and discriminate among a high quality (*V.*  
205 *unguiculata*, black-eyed bean) and a low quality (*Cicer arietinum*: Chick pea) host species<sup>41</sup>  
206 in the exact same type of arena and set-up (Fig. 1, Fig. S1). To make sure that females were  
207 motivated to search for hosts, they were mated with conspecific males 24 hours prior to the  
208 trials, and prevented from laying eggs by depriving them of host seeds. In contrast to male  
209 trails, host seeds did not need to be glued to stay in their place. Host seeds were also removed

210 between each female trail as eggs were laid readily by females and the presence of eggs on  
211 the hosts can affect female egg laying behaviour (heavily laden seeds are more often  
212 rejected). We registered female host inspection as behaviour. This inspection behavior was  
213 usually in form of females being on top of seeds making tactile contact with or ovipositing on  
214 the seed. Females readily laid eggs on both types of hosts during the assays, although this was  
215 never quantified. Similarly to the male assays, our scoring of behaviour captures variation in  
216 female cognition in terms of i) spatial orientation and memory as well as ii) chemo-sensory  
217 cues associated with host discrimination.

218

### 219 *Scoring behavior*

220 The observer (JdA) was always blinded to which line and evolution regime that was assayed.  
221 Each group of four beetles were scored for their behaviour as a group through three 10  
222 minute trails with a 20 minute acclimation period in a 30mm diameter petri dish before and  
223 in-between each trail. We could thus study overall differences in beetle cognition in terms of  
224 the average performance over time in each line and sex, as well as the potential for cognitive  
225 learning by looking at the improvement in performance within and between trails. We used  
226 two heating plates, each with one of the two color schemes (Fig. S1). The heating plates were  
227 run interchangeably (during the other plate's acclimation periods), and each line was scored  
228 once on each plate/color scheme per sex, resulting in 12 arena replicates per sex and line.  
229 Thus, 48 males and 48 females from each of the 6 lines were scored for behaviour over three  
230 consecutive 10 minute trails for a total of 17.280 behavioral observations.

231

### 232 *Statistics*

233 Male and female data were of the same form and were first analysed separately in equivalent  
234 models. We modelled the response as an “error rate” (the fraction of incorrect choices) over

235 the trails using a binomially distributed response variable with the levels “male/female” (male  
236 assays) or “good host/bad host” (female assays). Time of the trail was included as a covariate  
237 that was linearized by taking its natural logarithm prior to analysis. Evolution regime and trail  
238 number were analysed as discrete factors. We included interactions among all three of these  
239 explanatory variables, where two or three-way interactions including evolution regime would  
240 signify differences in performance over time among the two evolution regimes, indicative of  
241 an effect of sexual selection on cognitive learning. A main effect of evolution regime, on the  
242 other hand, would indicate an effect of sexual selection on general cognitive performance in  
243 the given task. Line identity was included as a random effect crossed with the three  
244 explanatory variables to account for the true replication of the experiment (being the six line  
245 replicates, and not individual observations). We included assay identity (the four beetles run  
246 together over consecutive trails) as an additional random effect. We also modelled main  
247 effects of heating plate to control for spatial effects in the lab and beetle color preferences.  
248 However, this effect was never significant and was ultimately removed from all models.

249

250 In addition to the male- and female-specific model, we also looked more formally for sex-  
251 differences in the response of cognitive performance to experimental evolution under  
252 alternative mating systems. This was done by recoding the levels of the response variable to  
253 “correct” and incorrect” and then running a statistical model with the main effect of “sex”  
254 crossed by the three other explanatory variables of interest (time, trail number and evolution  
255 regime) and the random effect of line identity.

256

257 Analyses were carried out with the package lme4<sup>48</sup> in the statistical software R. We used the  
258 “bobyqa” optimizer to increase the number of iterations (to 100.000) to achieve convergence  
259 of all models. We report type-II P-values based on likelihood ratio tests and  $\chi^2$ -statistics.

## 260 **Results**

### 261 *Cognitive performance of males*

262 Throughout the time of the trials, males increased the fraction of mounting attempts on  
263 females ( $\chi^2_{1}= 80.1$ ,  $P < 0.001$ ), suggesting that they learned the spatial location of females  
264 and then preferred to stay there to try to mate with them. While there was no main effect of  
265 trial, there was a strong interaction between trail and time ( $\chi^2_{2}= 18.7$ ,  $P < 0.001$ ) because  
266 males were more efficient in finding females already at the start of the third trail when  
267 trained, compared to the first trail when naïve. These results thus demonstrate clear effects of  
268 learning on performance in the mate searching task (Fig. 2A & C, Fig. S2). Males from the  
269 polygamy regime were more efficient overall in discriminating the sex of beetles compared to  
270 males from the monogamy regime ( $\chi^2_{1}= 8.56$ ,  $P = 0.003$ , Fig. 2A & C). This difference was  
271 mainly driven by the number of mounting attempts on reference males, which was much  
272 higher in males from monogamous lines (Fig. S2). However, there were no significant  
273 differences between selection regimes in how mate discrimination changed within or between  
274 trails (Fig. 2A & C, Table S2, Fig S2), indicating that learning was similar in the two  
275 evolution regimes (full statistics in Supplementary Table S2).

276

### 277 *Cognitive performance of females*

278 Throughout the time of the trials, females decreased the fraction of visits to suboptimal host  
279 seeds ( $\chi^2_{1}= 246.7$ ,  $P < 0.001$ ), suggesting that they learned the spatial location of the optimal  
280 host and then preferred to stay there to oviposit (Fig. 2B, D, Fig. S3). There was also a strong  
281 main effect of trial ( $\chi^2_{2}= 99.1$ ,  $P < 0.001$ ), as well as a strong interaction between trail and  
282 time ( $\chi^2_{2}= 33.8$ ,  $P < 0.001$ ), signifying that females improved in the host searching task  
283 through spatial and/or chemo-sensory learning (Fig. 2B, D, Fig. S3). However, contrary to  
284 the superior performance of polygamous lines in the male task, females from the two regimes  
285 did not show any overall differences in host search and discrimination (Table S3). This sex-

286 difference in the evolutionary response of cognitive performance was statistically significant  
287 ( $\chi^2_{1} = 5.91$ ,  $P = 0.015$ , Table S4). There were also no significant two-way interactions  
288 between selection regime and time or trail (Table S3), suggesting that female learning was  
289 largely similar in the two evolution regimes. There was, however, a marginally non-  
290 significant three-way interaction between selection regime, trail and time ( $\chi^2_{2} = 5.76$ ,  $P <$   
291  $0.056$ , Fig S3). This trend was driven by a pattern where evolution regimes showed very  
292 similar performance throughout the first trail as naïve beetles (regime:time interaction:  $\chi^2_{1} =$   
293  $0.02$ ,  $P = 0.89$ ), while monogamous lines tended to be better at discriminating between hosts  
294 when trained at the start of the third trail, but where this difference between regimes quickly  
295 disappeared as the trail went along (regime:time interaction:  $\chi^2_{1} = 4.28$ ,  $P = 0.039$ , Fig. S3).  
296 We note that this difference runs counter to the expectation that sexual selection should  
297 improve general cognitive abilities (full statistics in Supplementary S3 & S4).

298

### 299 *Sex-specific correlations between cognitive performance and lifetime reproductive success*

300 We explored the link between cognitive performance and fitness in each sex by calculating  
301 correlations between lifetime reproductive success (LRS, reported in<sup>46</sup>) and the measured  
302 cognitive traits (error rate in trail 1-3 and a learning score based on the relative reduction in  
303 error rate between the first and last trail:  $[e1 - e3] / e1$ ), based on trait means per sex and  
304 evolution line replicate. These correlations are graphically depicted in figure 4. We note that  
305 our interpretation here must remain tentative since these correlations are based only on 6  
306 data-points (three replicate lines per mating regime), and hence, cannot be used for rigorous  
307 statistical testing. Error rates are highly correlated between the three trails within each sex ( $r$   
308  $= 0.58-0.96$ ), suggesting substantial repeatability in behaviour among the six genotypes.  
309 However, error rates and the learning score are very weakly correlated between sexes ( $r = -$   
310  $0.08-0.34$ ), implying that different genes govern mate search in males and host search in

311 females. Moreover, while male LRS was negatively correlated to male error rates ( $r = -0.68 -$   
312  $-0.59$ ) and positively correlated to male learning ( $r = 0.59$ ) as predicted, it was positively  
313 correlated to the female error rate ( $r = 0.30-0.62$ ) and negatively correlated to female learning  
314 ( $r = -0.51$ ). This may suggest genetic conflict between the sexes at loci encoding the studied  
315 cognitive traits. Finally, female learning was negatively correlated to female LRS on both the  
316 focal ancestral host (black eyed bean;  $r = -0.68$ ) as well as an alternative host<sup>46</sup> (adzuki bean;  
317  $r = -0.71$ ), suggesting that cognitive learning may trade-off against fecundity in females.

318

## 319 **Discussion**

320 It is well known that sexual selection can put demands on cognitive abilities related to sexual  
321 signalling and mate choice<sup>5,16-18</sup> and mate search has also been linked to spatial learning in  
322 both vertebrates<sup>49</sup> and insects<sup>50</sup>. For example, in guppies, females from lines selected for  
323 larger brains were better at choosing among high and low quality mating partners<sup>51</sup> and males  
324 from the same lines were better at finding mates in a spatial learning task<sup>52</sup>. Similarly, in fruit  
325 flies, cognitive learning improves female mate choice<sup>18</sup>. However, whether the mating system  
326 can drive species differences in general cognition<sup>13</sup> is much more disputed and direct  
327 evidence remains scarce. Here we have shown that mating system variation can lead to the  
328 evolution of cognitive performance. Males evolving under polygamy were more efficient in  
329 directing their mating effort towards females in spatially complex mixed-sex settings. Given  
330 that these males also have higher reproductive success than males evolving under  
331 monogamy<sup>46</sup>, this suggests that increased cognitive performance in mate search has fitness  
332 benefits in males (see also Fig. 4). However, the evolved increase in mate search ability was  
333 not accompanied by improved learning or increases in female cognitive performance, as  
334 expected under the mating mind hypothesis.

335

336 These negative results are readily interpretable as there was sufficient power in our design to  
337 detect significant differences in male performance between evolution regimes, as well as to  
338 demonstrate substantial improvement in the cognitive tasks through learning in both males  
339 and females (Figs. 2 & 3). Our main results thus imply that good genes processes resulting in  
340 overall improvement of cognitive ability may not materialize when sexual selection acts on  
341 standing genetic variation, as it did in our experiment. Interestingly, the decreased ability of  
342 monogamous males (relative to polygamous males) to avoid directing mating attempts  
343 toward other males was drastic and evolved in only 35 generations of relaxed sexual selection  
344 (Fig. S2). This fast decrease implies that selection acted on segregating genetic variation with  
345 antagonistic pleiotropic effects on other fitness related traits, because i) decreases in  
346 monogamous lines due to the accumulation of de novo mutation over such short time frames  
347 seem unlikely, and ii) effects of genetic drift should be negligible since effective population  
348 size was relatively large ( $N_e \sim 150$ ), all three replicate lines for each regime showed parallel  
349 divergence (Fig 2A & C, Fig. 3) and the effect of drift was controlled for in the applied  
350 statistical models. Our results thus also pose the question of what maintains such vast  
351 amounts of genetic variation in male cognitive behaviour.

352

353 Our results are in many ways similar to the study by Hollis and Kawecki (2014) on  
354 *Drosophila melanogaster* fruit flies, which is the only other study we know of that has  
355 applied experimental evolution and manipulated the mating system to look at effects on  
356 cognitive abilities. In their study, evolution under polygamy contributed to the maintenance  
357 of mate acquisition abilities in males, but also lead to superior aversive learning - a cognitive  
358 task not directly related to the applied sexual selection. While this suggests that sexual  
359 selection improved general cognitive abilities, in line with the mating mind hypothesis,  
360 polygamous females showed no such increase, and even tendencies for reduced cognitive

361 performance relative to females from monogamous lines<sup>53</sup>. This is also in line with our  
362 results, showing no differences in performance between monogamous and polygamous *C.*  
363 *maculatus* females overall, and a tendency for monogamous females to learn faster (Fig. S3).

364

365 Indeed, as an alternative to good genes effects, sexual selection may lead to sex-limited  
366 responses and increased sexual dimorphism in cognition<sup>13,19,49,54,55</sup>. Such an outcome is  
367 expected when males and females experience different selection pressures and genetic  
368 constraints are not insurmountable<sup>56</sup>, so that cognitive traits can evolve independently in each  
369 sex<sup>19</sup>. One mechanistic explanation for the sex-specificity observed in this study could be  
370 differences in the chemosensory machinery required to successfully identify and discriminate  
371 the sex of mating partners and host species (in males and females respectively). Given that  
372 collecting and processing such information should require costly development and  
373 maintenance of neuroreceptors<sup>4,50</sup>, cognitive performance in mate search and host search may  
374 trade-off against each other, if different receptors are employed for the two tasks and these  
375 receptors compete for resources, physical space, or downstream cognitive processing of their  
376 transmitted information. This hypothesis is in line with the tendency for sexual selection to  
377 have positive effects on male mate search but slightly negative effects on female cognitive  
378 learning in both our study and Hollis and Kawecki's (2014) study on fruit flies. Moreover, in  
379 this population of beetle, female fecundity has previously been shown to be negatively  
380 correlated to the accuracy of male sex discrimination<sup>40</sup>, and in this study, female host search  
381 and discrimination tended to be negatively correlated to male reproductive success (Fig. 4).

382

383 These results imply that selection on cognitive traits may sometimes act with opposing forces  
384 in the sexes. If in such cases genetic constraints are preventing each sex from evolving  
385 independently from the other<sup>56,57</sup>, this type of sexual antagonism<sup>58</sup> will generate balancing



386 selection that can act to maintain allelic variation at genes underpinning cognitive  
387 abilities<sup>59,60</sup>. Mechanistically, sexual antagonism over cognitive traits could, for example,  
388 arise if males benefit mostly from increasing allocation to one type of chemoreceptor (e.g.  
389 increasing accuracy of sex discrimination) while females benefit from allocation to another  
390 type of receptor (e.g. increasing accuracy of host discrimination). Sexual antagonism could  
391 also arise if the benefit of a specific cognitive ability is limited mainly to one sex while its  
392 energetic cost is paid by both sexes, as seen for other types of traits under sexually  
393 antagonistic selection<sup>40,61,62</sup>. In this study, female learning correlated negatively with both  
394 male and female reproductive success (Fig. 4), in line with this hypothesis.

395

396 Indeed, cognitive traits and learning are generally assumed to come with energetic costs. For  
397 example, there are cost of developing and using a large brain in vertebrates<sup>7,9,63</sup>, as well as  
398 documented costs of memory and allocation to cognitive traits in insects<sup>4,50,64–66</sup>. Similarly,  
399 sexually selected traits are themselves expected to be costly<sup>17,24,27,67</sup>, and while some studies  
400 have found a positive genetic correlation between primary and secondary sexual traits and  
401 brain size (e.g.<sup>68,69</sup>), in line with good genes effect, there are also examples of negative  
402 correlations (e.g.<sup>22</sup>), suggesting that increased sexual selection may sometimes lead to  
403 decreases in cognitive traits via energy allocation trade-offs<sup>24,70,71</sup>. The action of such  
404 antagonistic pleiotropy within and between sexes to maintain genetic variation could thus be  
405 responsible for the substantial amounts of standing genetic variation in male sex  
406 discrimination documented here and previously<sup>40</sup> in this population of *C. maculatus*. The  
407 notion that sexually antagonistic selection has played a key role in this process is also  
408 supported by previous studies on the population<sup>40,44,72,73</sup>.

409

410 Behavioral plasticity can play an important role in deciding species distributions, persistence  
411 and modes of adaptation to changing environments, for example by increasing the efficacy of  
412 spatial exploration and resource sampling mediating niche matching<sup>1-5</sup>. Cognitive processes  
413 are also key in mate choice dynamics and may therefore play a role in speciation<sup>74-79</sup>. The  
414 interplay between sexual selection and the evolution of cognition, with special emphasis on  
415 potentially underappreciated effects of sexually antagonistic selection on cognitive traits, may  
416 therefore have important consequences for evolutionary dynamics and certainly deserves  
417 more attention in other study systems. While the mating mind and good genes hypothesis  
418 predict a positive association between cognitive ability and the strength of sexual selection to  
419 be built up by purifying selection against recurrent deleterious pleiotropic mutations, our  
420 study implies that much of the standing genetic variation in cognitive performance upon  
421 which evolutionary responses to novel environments rely, will have been moulded and  
422 maintained by forces of balancing selection within and between the sexes. This sets the stage  
423 for rapid sex-specific responses to changes in ecological and socio-sexual conditions.

424

425

426 **Competing interests**

427 The authors report no competing interests

428

429 **Ethics statement**

430 All experiments have been carried out within the regulations held by Swedish governmental  
431 laws. Actions were taken to reduce the number of beetles used in the study.

432

433 **Data accessibility:**

434 Data will be uploaded to the Dryad Data Repository upon potential acceptance

435

436 **Author's contributions**

437 The study was conceived by JB, JdA and DB, and was carried out by JdA and JB. DB  
438 analyzed the data and wrote the manuscript. All authors commented on the first draft.

439

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442 experimental evolution lines. We also like to thank Johanna Liljestränd-Rönn for practical  
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447

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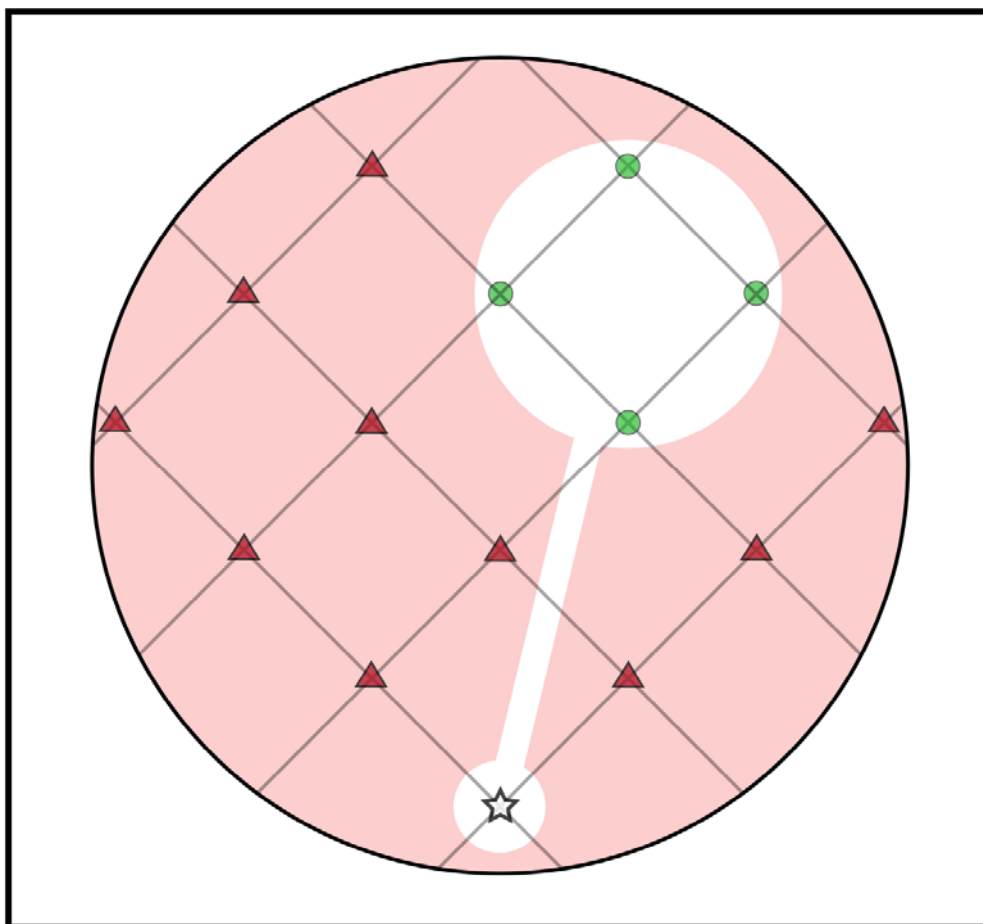


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620 **Figure 1:** The experimental arena (a 150 mm diameter petri-dish) used for the behavioural  
621 assays. The symbols indicate the following: white star = place where the four focal  
622 individuals were placed at the start of each trail; red triangles = the wrong choice (males for  
623 male trails | chick-peas for female trails), green circles = the correct choice (females for male  
624 trails | black-eyed beans for female trails).

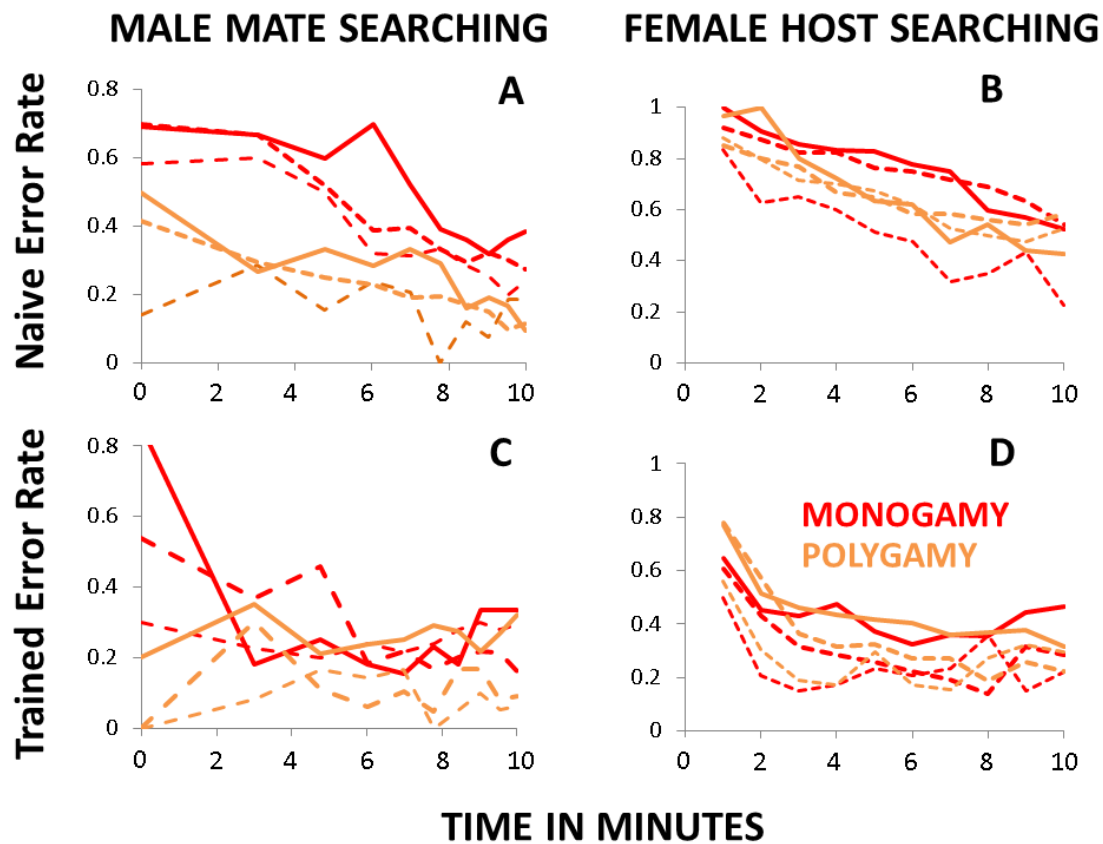
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627 **Figure 2:** Sex-specific baseline cognitive performance and learning in the three replicate  
628 monogamous (red) and polygamous (orange) lines. Male mate searching ability (A, C) and  
629 female host searching ability (B, D) in terms of “error rates” (the fraction of male mating  
630 attempts with other males, and the fraction of female contacts with the suboptimal host).  
631 Shown are data for naïve beetles (A, B) in the first 10-minute trail, and trained beetles (C, D)  
632 in the third 10-minute trail. The line type (thick and full to thin and hatched) designates the  
633 line identity and makes it possible to match line performance across the first and the third  
634 trail.

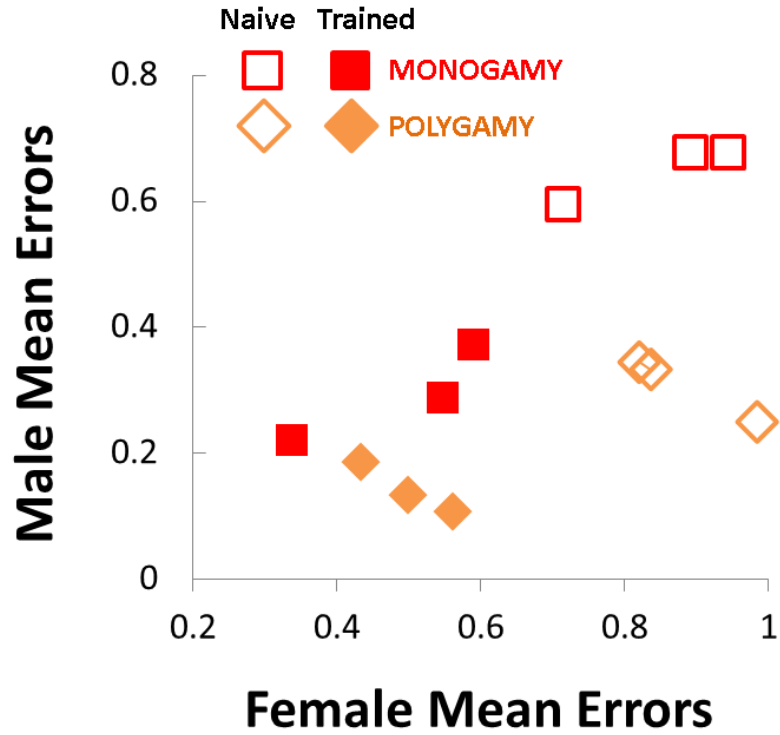
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637 **Figure 3:** Cognitive performance (in terms of error rates) averaged over the full 10-minute  
638 trial, for naïve beetles in the first trail (open symbols) and trained beetles in the third trail  
639 (closed symbols). Mean male and female error rates are shown for each of the three replicate  
640 monogamous (red) and polygamous (orange) lines.

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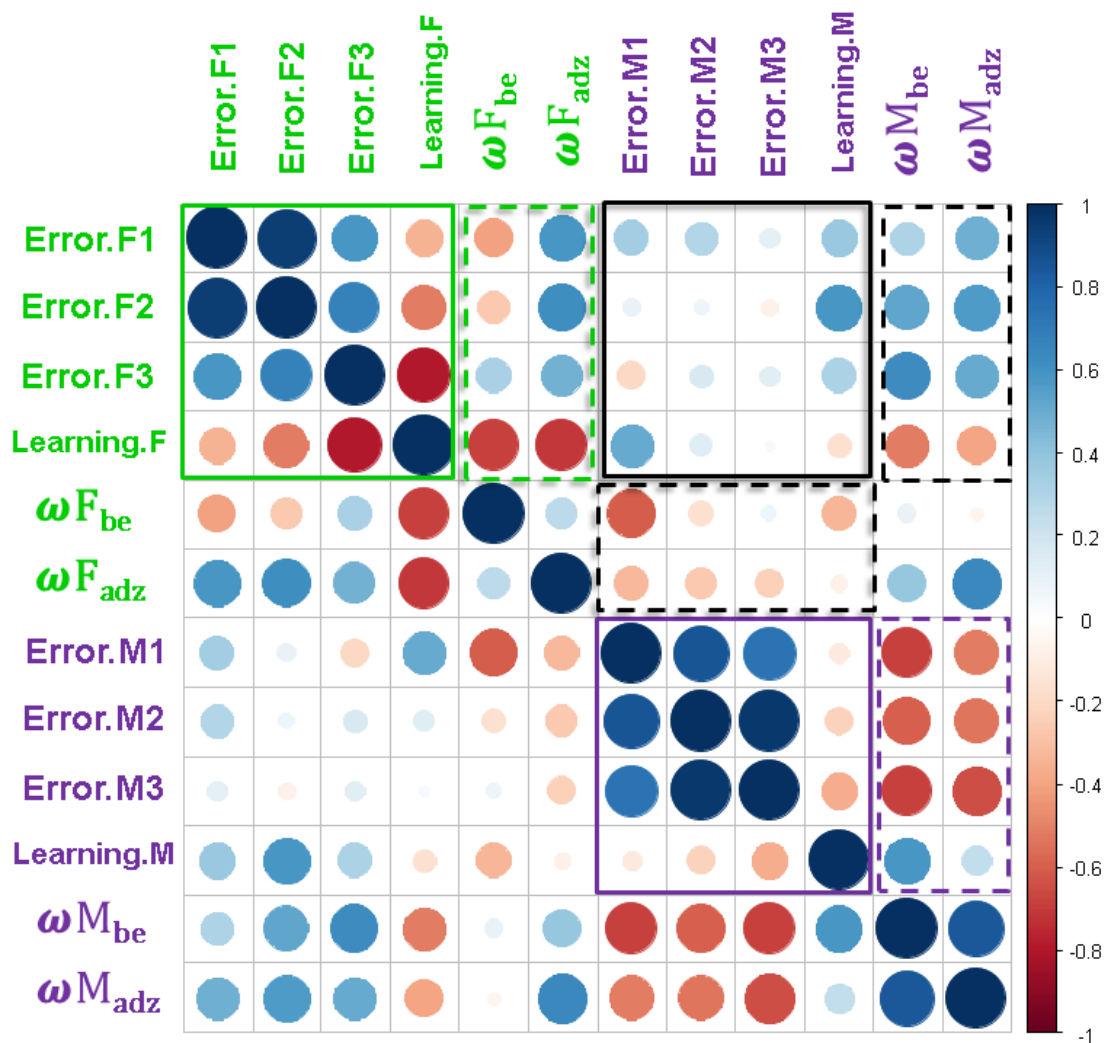


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644 **Figure 4:** Sex-specific genetic correlations between cognitive performance and lifetime  
 645 reproductive success. Shown are correlations based on the 6 lines (3 from each regime)  
 646 between cognitive performance (error rates in the three consecutive behavioral trails and a  
 647 measure of learning from trail 1 to 3:  $[E1-E3]/E1$ ), and lifetime reproductive success ( ) on  
 648 two host species (be = ancestral black eyed beans, adz = adzuki beans). Within-sex genetic  
 649 correlations are highlighted by green (F = female) and purple (M = male) squares. Black  
 650 squares highlight between-sex genetic correlations. Full lines designate correlations between  
 651 measures of cognitive performance and hatched lines between cognitive performance and  
 652 lifetime reproductive success. Note that the same correlations are depicted both above and  
 653 below the diagonal. Circles on the diagonal are trait variances standardized to a size = 1.

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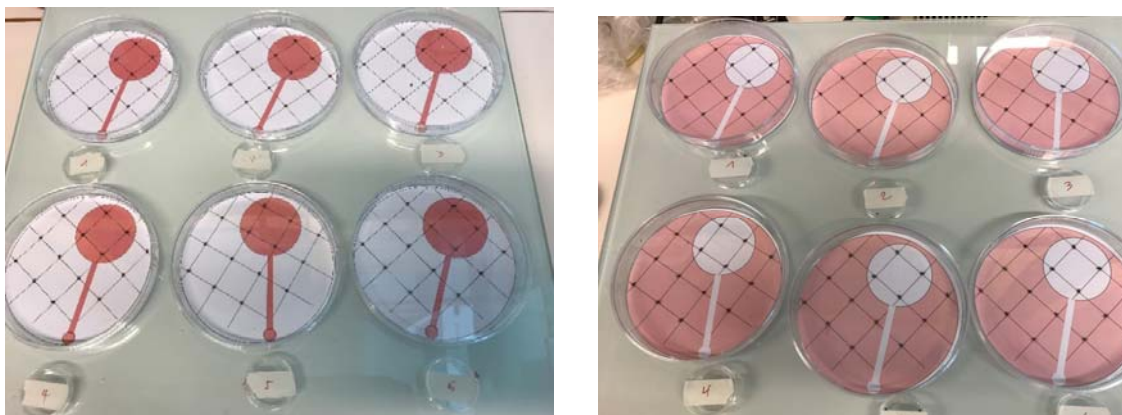
## Supplementary Material:

659

### 660 **Figure S1: Experimental arenas**

661 Arenas used to assess cognition and learning. Shown are the two arena types with reversed  
662 color schemes, placed on heating plates situated ca. 1 metre apart. Below the arenas are the  
663 30mm diameter acclimation petri-dishes where the four focal beetles spent 20 minutes prior  
664 to and in-between trails.

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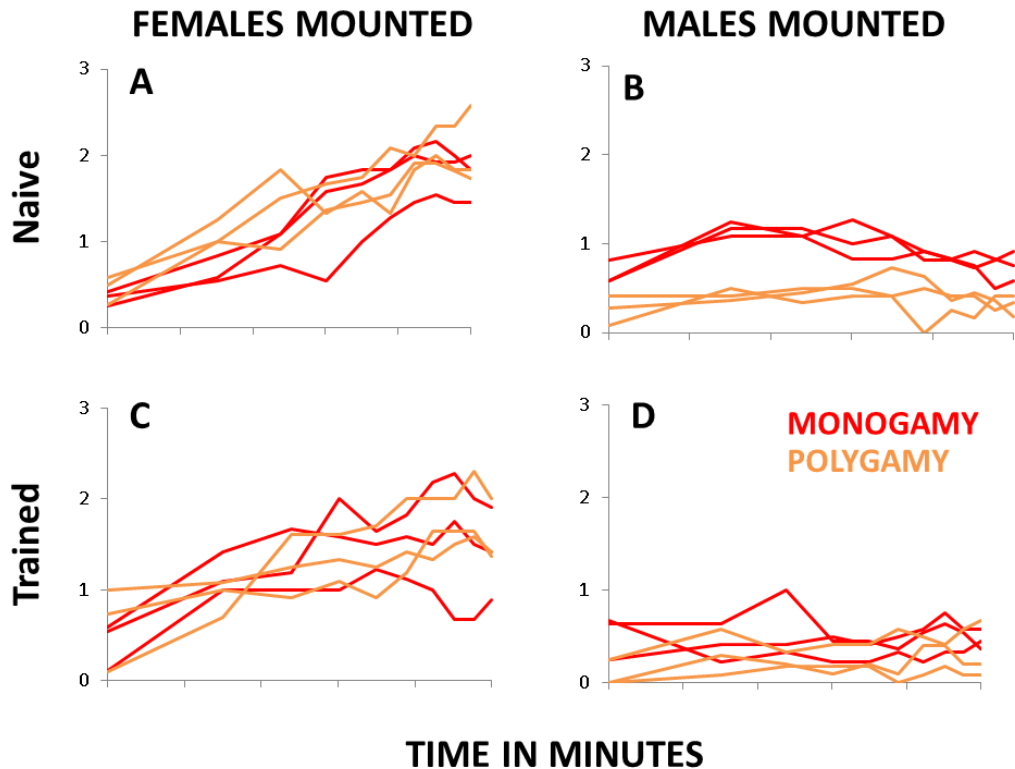
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669 **Figure S2: Male cognitive performance**

670 The averaged summed number of times that the four males made mounting attempts on  
 671 females (left; A & C) and males (right; B & D) during the first (“Naïve” beetles)  
 672 (“Trained” beetles) behavioural trail.

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677 **Table S2: Male cognitive performance**

678 Type II Wald chi-square tests

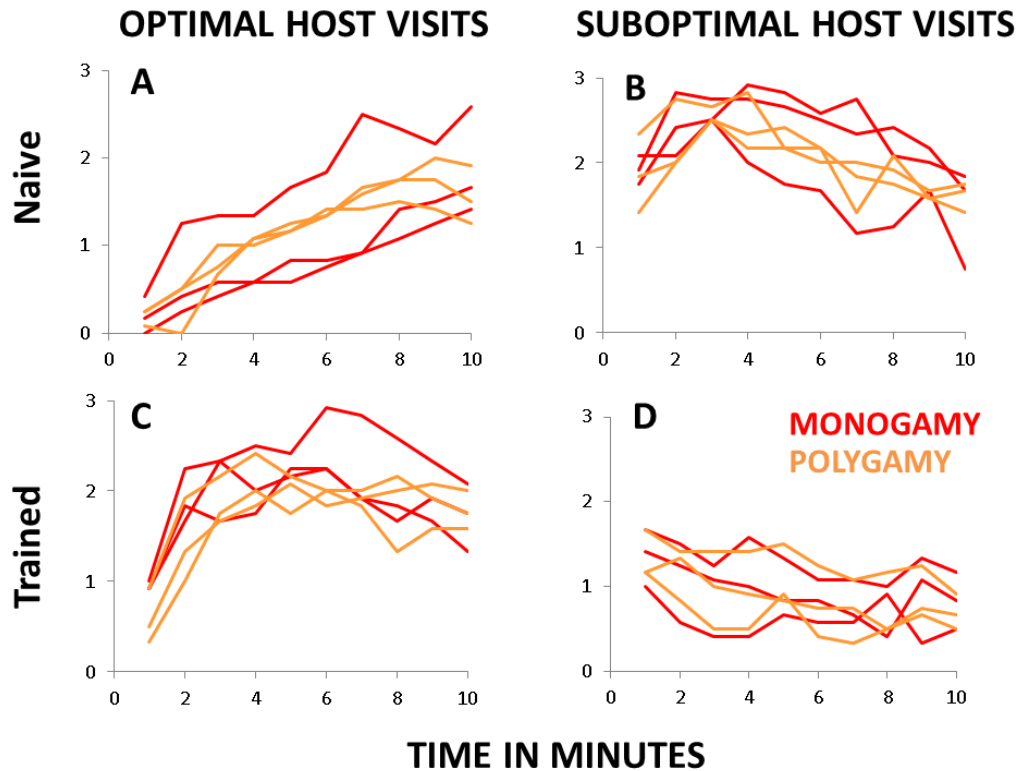
	Chisq	Df	P	
trial	4.2328	2	0.120466	
time	80.0619	1	< 2.2e-16	***
regime	8.5645	1	0.003428	**
trial:time	18.7180	2	8.619e-05	***
trial:regime	3.8489	2	0.145959	
time:regime	2.3646	1	0.124115	
trial:time:regime	0.1789	2	0.914416	



679 **Figure S3: Female cognitive performance**

680 The averaged summed number of times that the four females made inspections of optimal  
 681 black-eyed beans (left; A & C) and sub-optimal chick-peas (right; B & D) during the first  
 682 (“Naïve” beetles) and third (“Trained” beetles).

683



684

685

686 **Table S3: Female cognitive performance**

687

Type II Wald chi-square tests

	Chisq	Df	P	
trial	99.0967	2	< 2.2e-16	***
minuteLOG	246.7218	1	< 2.2e-16	***
sel	0.0614	1	0.80431	
trial:minuteLOG	33.7639	2	4.659e-08	***
trial:sel	0.5165	2	0.77240	
minuteLOG:sel	0.2564	1	0.61259	
trial:minuteLOG:sel	5.7561	2	0.05624	.

688 **Table S4: Sex differences in cognitive performance**

689

	Chisq	Df	P	
690 <b>sex</b>	<b>69.4112</b>	<b>1</b>	<b>&lt;2.2e-16</b>	<b>***</b>
trial	64.0866	2	1.213e-14	***
691 time	375.9454	1	<2.2e-16	***
regime	1.1411	1	0.285412	
692 <b>sex:trial</b>	<b>21.9326</b>	<b>2</b>	<b>1.727e-05</b>	<b>***</b>
<b>sex:time</b>	<b>12.3163</b>	<b>1</b>	<b>0.000449</b>	<b>***</b>
693 trial:time	52.6199	2	3.747e-12	***
<b>sex:regime</b>	<b>5.9118</b>	<b>1</b>	<b>0.015040</b>	<b>*</b>
694 trial:regime	3.1970	2	0.202196	
time:regime	0.1909	1	0.662209	
695 sex:trial:time	0.4299	2	0.806599	
sex:trial:sel	2.0383	2	0.360893	
696 sex:time:regime	2.3276	1	0.127096	
trial:time:regime	3.6235	2	0.163366	
697 sex:trial:time:regime	2.7250	2	0.256015	

698

699