

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, adaptation¹⁻⁴. 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 cognition⁵⁻¹⁰. One such hypothesis is the idea that
44 the social system of a species is particularly important in shaping cognitive abilities¹¹. Indeed,
45 the complex social structure of human societies has been suggested as a main driver of our
46 species' intelligence¹². 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*")^{13,14}.

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 systems¹⁵, suggesting that the mating mind
56 hypothesis could be generalized to explain variation among non-human taxa¹⁶. Indeed, the
57 idea that sexual selection requires cognitive abilities has been widely explored (e.g. ^{5,14,16-18}).
58 However, comparative evidence for a direct link between mating system variation and animal
59 cognition is mixed^{16,17,19}. For example, in primates monogamy rather than polygamy is
60 associated with larger brain size²⁰, 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^{5,11}.

63 In both primates⁶ and birds²¹, 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 fidelity²², 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 methods²³ 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^{17,24}, 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”)²⁵. Since most new mutations are
81 thought to be deleterious and have wide ranging pleiotropic effects on fitness related traits²⁶,
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 daughters²⁷. 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 occurs²⁸. Beetles emerging from seeds are reproductively mature and require neither water
108 nor food to reproduce (e.g.^{28,29}). Adults typically die in 7-14 days after emergence in the
109 absence of food or water (e.g.³⁰).

110

111 Sexual selection is intense in this species, including both pre- and post-copulatory
112 processes³¹⁻³⁶. 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^{28,31,37-39}. 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 females⁴⁰, who when mated often hide amongst the
118 beans to escape costly re-mating attempts by males³⁴⁻³⁶.

119

120 Female host plant search and discrimination is complex. *C. maculatus* has a wide repertoire
121 of fabaceous host plants⁴¹ but females have a clear host hierarchy and preference, and they
122 discriminate between high quality and low quality species (e.g. ^{42,43}). 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^{38,43}.

127

128 The experimental evolution lines (see below) come from a genetic stock recently isolated
129 from the wild⁴⁴. *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^{38,41,43}. 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. ⁴⁵).

136

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

138 The lines used in this study are thoroughly described in Martinossi-Allibert et al.⁴⁶. 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 plant⁴¹ *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 competition⁴⁶. 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 lines⁴⁶.

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 population⁴⁰). 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:⁴⁰, as in
201 many other insects⁴⁷).

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 species⁴¹
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 lme4⁴⁸ 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 χ^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 in⁴⁶) 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 host⁴⁶ (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^{5,16-18} and mate search has also been linked to spatial learning in
322 both vertebrates⁴⁹ and insects⁵⁰. For example, in guppies, females from lines selected for
323 larger brains were better at choosing among high and low quality mating partners⁵¹ and males
324 from the same lines were better at finding mates in a spatial learning task⁵². Similarly, in fruit
325 flies, cognitive learning improves female mate choice¹⁸. However, whether the mating system
326 can drive species differences in general cognition¹³ 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 monogamy⁴⁶, 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 lines⁵³. 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^{13,19,49,54,55}. Such an outcome is
367 expected when males and females experience different selection pressures and genetic
368 constraints are not insurmountable⁵⁶, so that cognitive traits can evolve independently in each
369 sex¹⁹. 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^{4,50}, 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 discrimination⁴⁰, 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^{56,57}, this type of sexual antagonism⁵⁸ will generate balancing

386 selection that can act to maintain allelic variation at genes underpinning cognitive
387 abilities^{59,60}. 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^{40,61,62}. 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^{7,9,63}, as well as
398 documented costs of memory and allocation to cognitive traits in insects^{4,50,64–66}. Similarly,
399 sexually selected traits are themselves expected to be costly^{17,24,27,67}, and while some studies
400 have found a positive genetic correlation between primary and secondary sexual traits and
401 brain size (e.g.^{68,69}), in line with good genes effect, there are also examples of negative
402 correlations (e.g.²²), suggesting that increased sexual selection may sometimes lead to
403 decreases in cognitive traits via energy allocation trade-offs^{24,70,71}. 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 previously⁴⁰ 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^{40,44,72,73}.

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 matching¹⁻⁵. Cognitive processes
413 are also key in mate choice dynamics and may therefore play a role in speciation⁷⁴⁻⁷⁹. 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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444

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447

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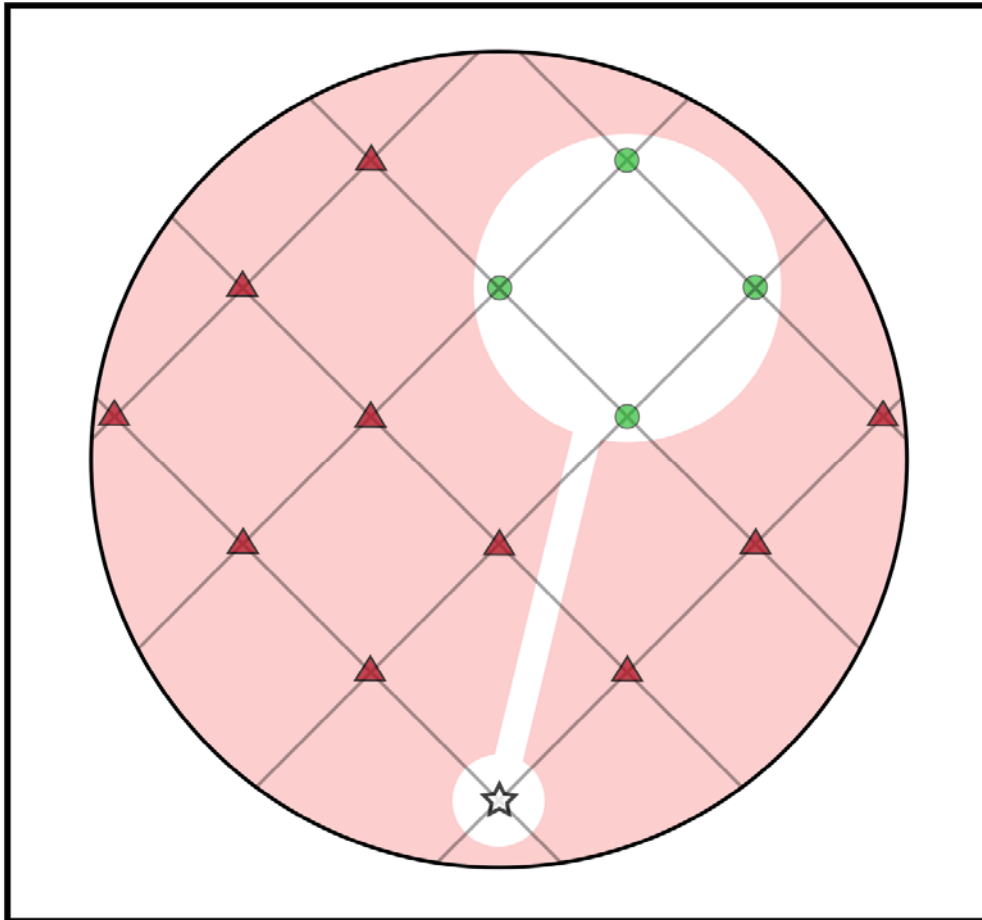
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620 **Figure 1:** The experimental arena (a 150 mm diameter petri-dish) used for the behavioural
621 assays. The symbols indicate the following: white star = place where the four focal
622 individuals were placed at the start of each trail; red triangles = 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).

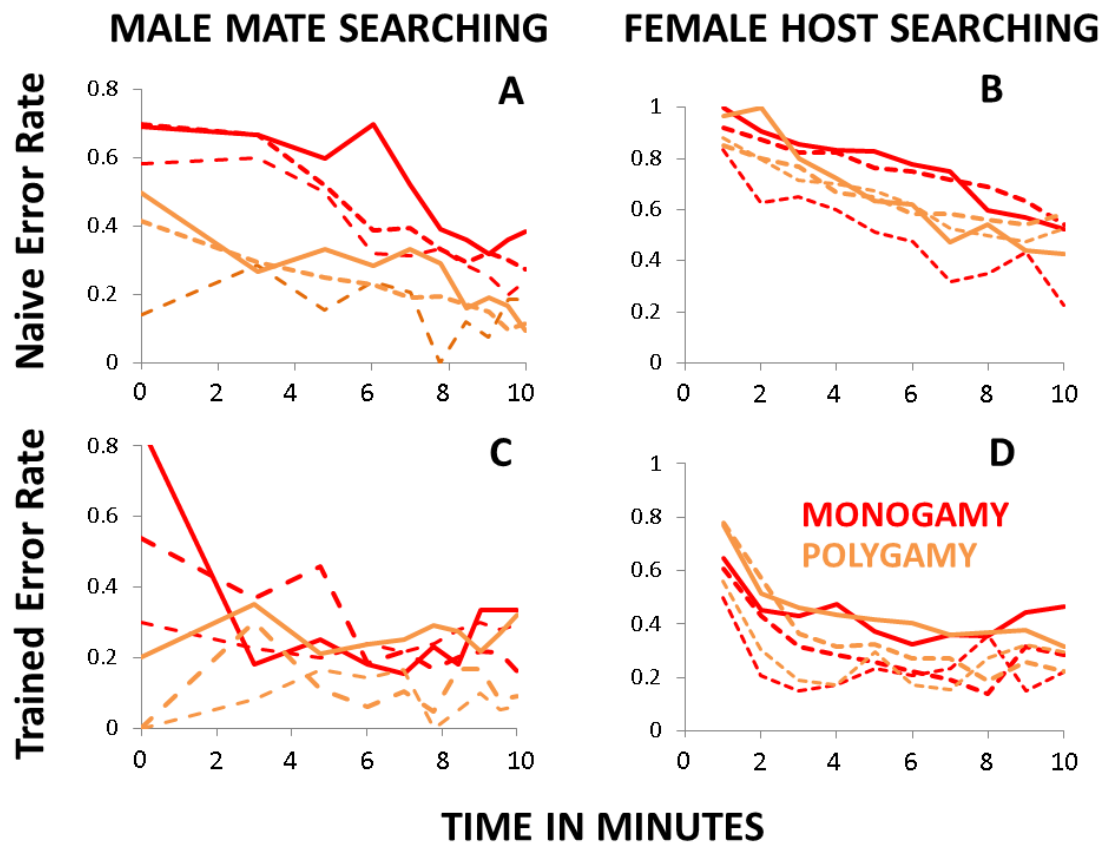
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627 **Figure 2:** Sex-specific baseline cognitive performance and learning in the three replicate
628 monogamous (red) and polygamous (orange) lines. Male mate searching ability (A, C) and
629 female host searching ability (B, D) in terms of “error 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.

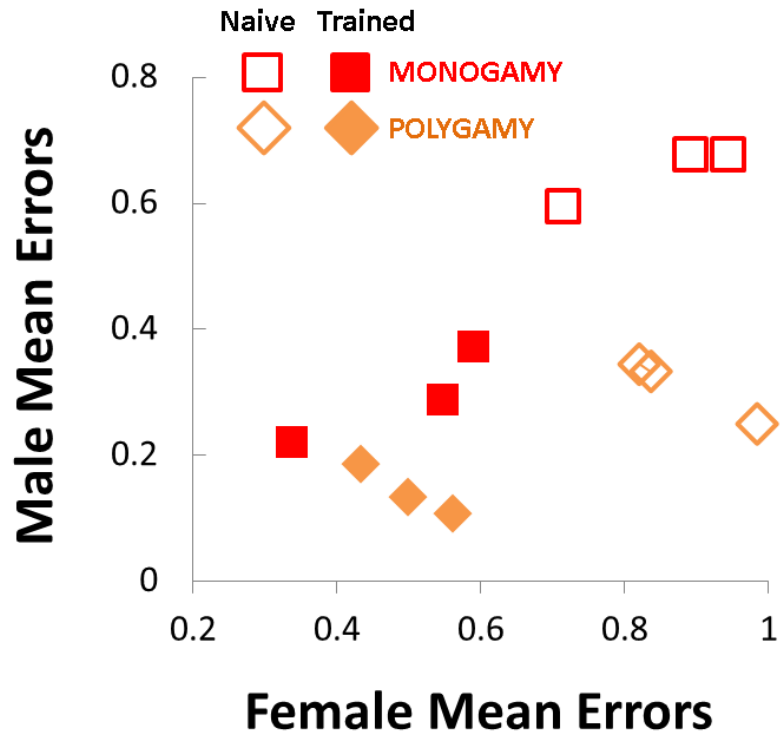
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637 **Figure 3:** Cognitive performance (in terms of error rates) averaged over the full 10-minute
638 trial, for naïve beetles in the first trail (open symbols) and trained beetles in the third trail
639 (closed symbols). Mean male and female error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

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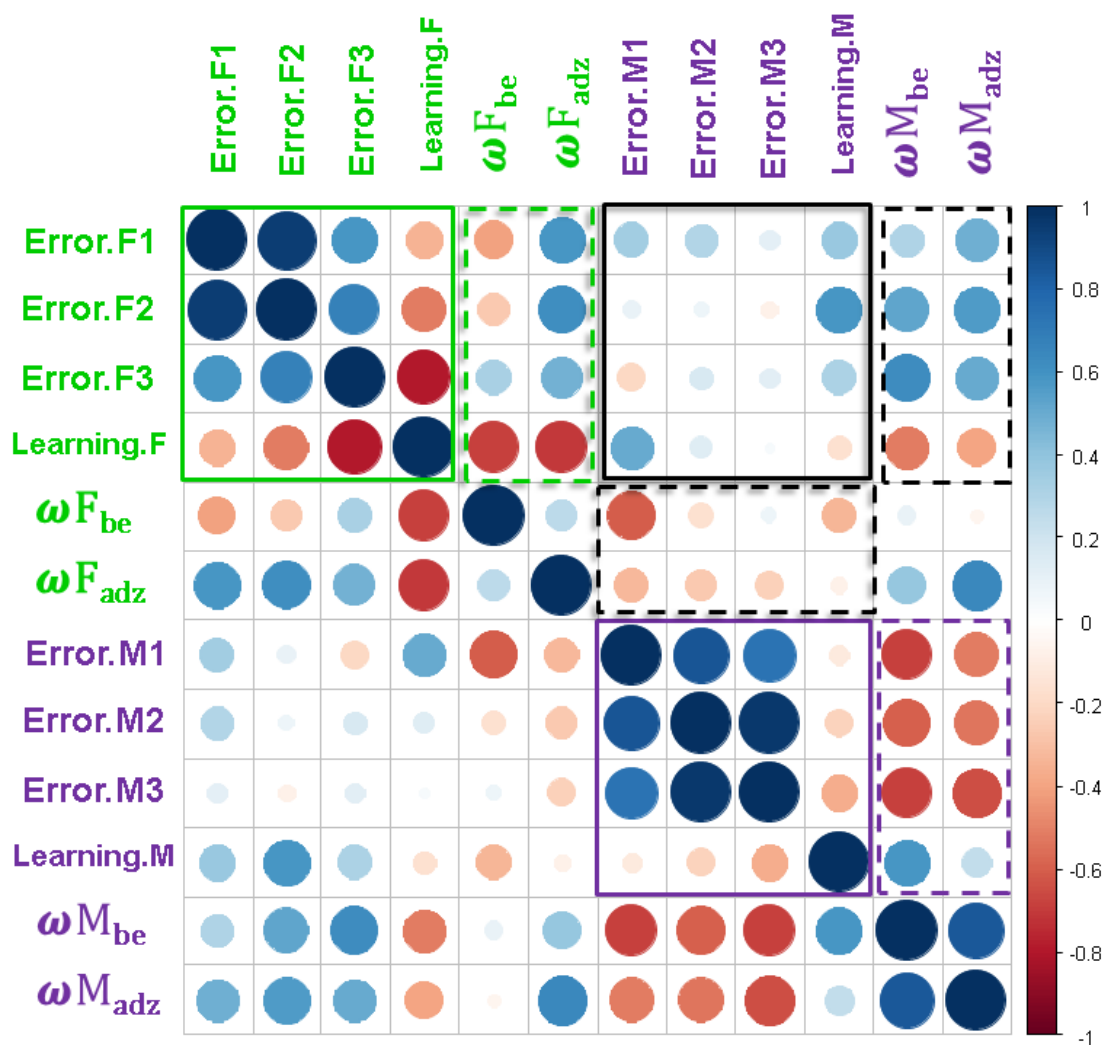


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644 **Figure 4:** Sex-specific genetic correlations between cognitive performance and lifetime
 645 reproductive success. Shown are correlations based on the 6 lines (3 from each regime)
 646 between cognitive performance (error rates in the three 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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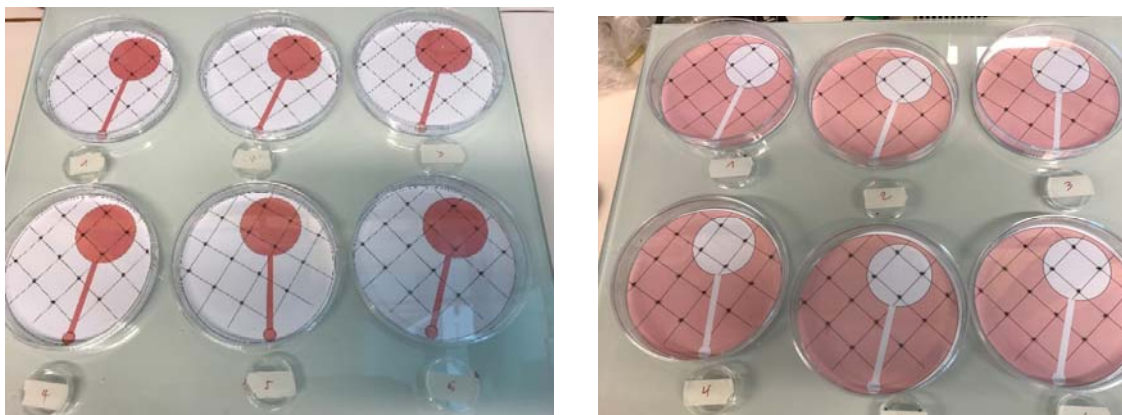
Supplementary Material:

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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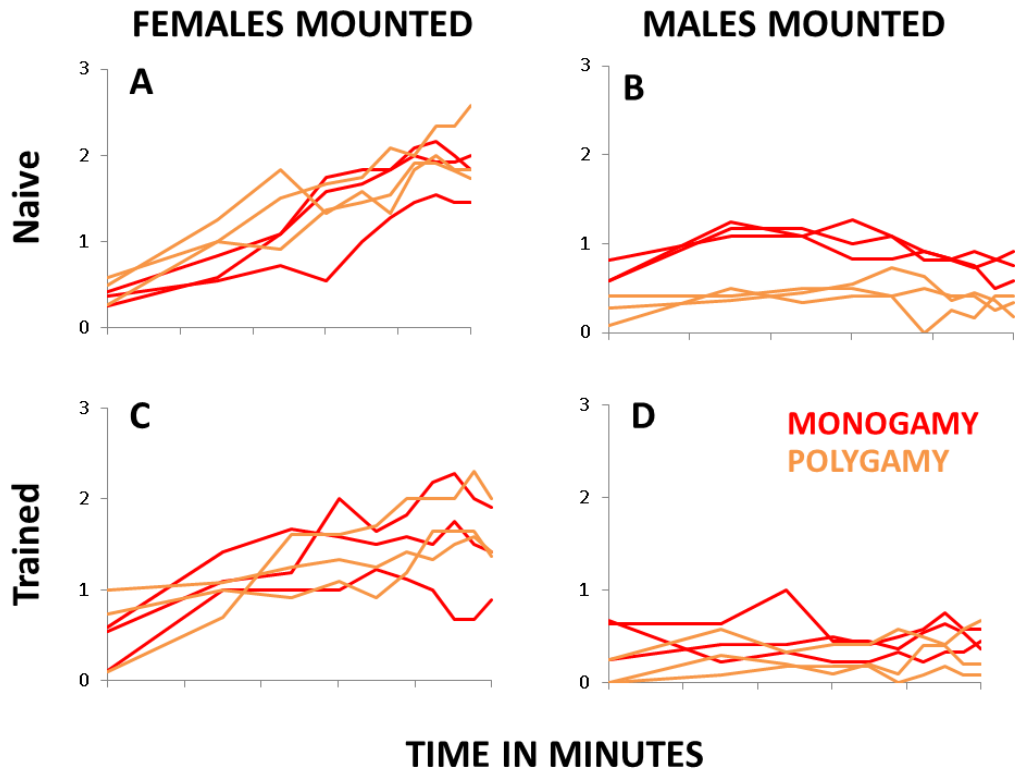
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669 **Figure S2: Male cognitive performance**

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**

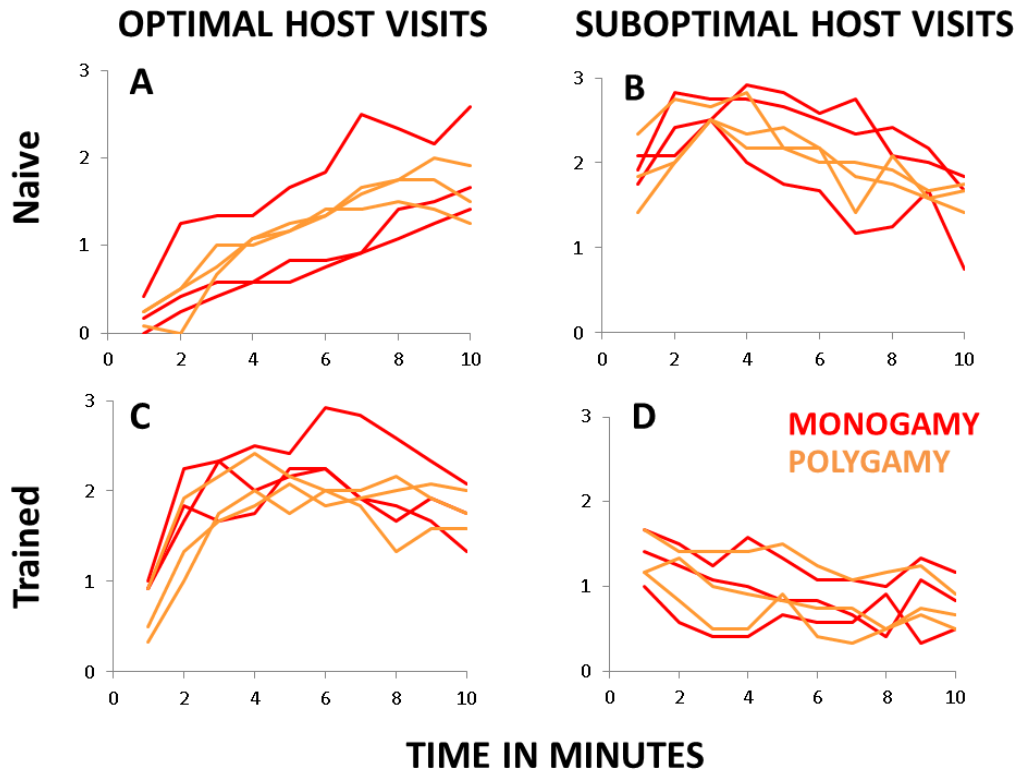
678 Type II Wald chi-square tests

	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 sex	69.4112	1	<2.2e-16	***
trial	64.0866	2	1.213e-14	***
691 time	375.9454	1	<2.2e-16	***
regime	1.1411	1	0.285412	
692 sex:trial	21.9326	2	1.727e-05	***
sex:time	12.3163	1	0.000449	***
693 trial:time	52.6199	2	3.747e-12	***
sex:regime	5.9118	1	0.015040	*
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