

## Problem solving 1

A battle of wits? Problem-solving abilities in invasive Eastern grey squirrels and native Eurasian red squirrels.

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1 **ABSTRACT**

2 Behavioural flexibility has been argued to be an evolutionarily favourable trait that helps  
3 invasive species to establish themselves in non-native environments. But few studies have  
4 compared the level of flexibility (whether considered as an outcome or as a process) in  
5 mammalian invaders and related native species. Here, we tested whether flexibility differs  
6 between groups of free-ranging invasive Eastern grey squirrels (*Sciurus carolinensis*) and  
7 native Eurasian red squirrels (*S. vulgaris*) in the UK, using an easy and a difficult food-  
8 extraction task. All individuals of both species showed flexibility, at the outcome level, in  
9 solving the easy task and solution time was comparable between species across a series of  
10 successes. A higher proportion of grey squirrels than red squirrels solved the difficult task.  
11 However, for those squirrels that did solve the task, solving efficiency was comparable  
12 between species on their first success, and a few red squirrels outperformed the grey squirrels  
13 in subsequent successes. Between species analysis showed that instantaneous flexibility,  
14 flexibility at the process level that was measured as the rate of switching between tactics after  
15 a failed attempt, was higher in red squirrels than in grey squirrels. Within species analysis  
16 also revealed that red squirrel problem solvers showed higher flexibility at the process level,  
17 than their non-solver counterparts. Non-solvers also failed to make 'productive' switches  
18 (switching from ineffective tactics to effective tactics). Together, the results suggest that  
19 problem-solving ability overlaps in the two species, but is less variable, and on average  
20 higher, in grey squirrels than in red squirrels. The superior behavioural flexibility of the grey  
21 squirrels, shown here by success at problem solving, may have facilitated their invasion  
22 success, but it may also have resulted from selective pressures during the invasion process.  
23 *Keywords: behavioural flexibility, invasive and native species, problem solving, squirrels*

## 24 INTRODUCTION

25 Behavioural flexibility has been argued to be an evolutionarily favourable trait for  
26 invasive species, as flexibility helps them adapt to non-native environments (e.g. Jarić,  
27 Jaćimović, Cvijanović, Knežević-Jarić, & Lenhardt, 2014; Webb, Letnic, Jessop, &  
28 Dempster, 2014; Lefebvre, Reader, & Sol, 2013; Sol, Timmermans, & Lefebvre, 2002; Sol  
29 & Lefebvre, 2000). Flexibility has been measured in a number of ways (see review by Audet  
30 & Lefebvre, 2017), and it has been conceptualised at different levels. On the one hand, it has  
31 been conceived as a process (hereafter, ‘the process level’) through which animals are able to  
32 vary their behaviours (e.g. Benson-Amram & Holekamp, 2012; Chow, Lea, & Leaver, 2016;  
33 Chow, Lea, Hempel, & Robert, 2017; Griffin, Diquelou, & Perea, 2014). For example,  
34 Lefebvre and colleagues have measured flexibility from the incidence of novel foraging  
35 techniques per taxon (Lefebvre et al., 2013; Sol et al., 2002; Sol & Lefebvre, 2000). On the  
36 other hand, flexibility has been conceived as an outcome of actions observed when animals  
37 show variations in responding to challenges (hereafter, ‘the outcome level’). For example,  
38 flexibility could be measured as the outcome of success or failure in solving artificial  
39 problem-solving tasks (review by Griffin & Guez, 2014) in which animals are required to  
40 overcome obstacles to obtain food rewards, either by applying previously learned tactics to  
41 solve a novel problem, or by developing novel tactics to solve old problems (Kummer &  
42 Goodall, 1985; Reader & Laland, 2003). In practice, the process can be also inferred from its  
43 behavioural outcome, for example, enhanced flexibility is indicated by success in solving  
44 artificial problem tasks.

45

46 Both these approaches have been used to suggest a relationship between flexibility and  
47 success as an invasive species. Sol et al. (2002) and Sol and Lefebvre (2000) have shown  
48 that, across taxa, the incidence of novel foraging techniques reported is correlated with the

49 establishment of invasive bird species in new environments, while Griffin and Diquelou  
50 (2015) have used artificial problem-solving tasks to examine the level of flexibility in two  
51 successfully invasive bird species, Indian mynas (*Acridotheres tristis*) and noisy mynas  
52 (*Manorina melanocephala*). In the present paper, we take a more direct approach to the  
53 hypothesis of a relationship between flexibility and invasiveness, by comparing the  
54 flexibility, both at the outcome and at the process levels, shown by an invasive species and  
55 the native species it displaces.

56

57       Our study model was a population of free-ranging invasive grey squirrels (*Sciurus*  
58 *carolinensis*) and a population of native red squirrels (*S. vulgaris*) in the UK, and we  
59 compared their flexibility, at the outcome level, by measuring their success in solving food-  
60 extraction problems in field experiments. Although grey squirrels are larger than red squirrels  
61 (Bryce, Speakman, Johnson, & Macdonald, 2001), the two species share many morphological  
62 and ecological characteristics, so that niche overlap is high, see Koprowski (1994) for grey  
63 squirrels and Lurz, Gurnell, & Magris (2005) for red squirrels. Grey squirrels are regarded as  
64 one of the ‘100 World’s Worst Invasive Alien Species’ (Lowe, Browne, & Boudjelas, 2008).  
65 They were introduced to the UK and Ireland in the 19<sup>th</sup> century (Gurnell, 1987) and more  
66 recently to Italy (Bertolino, Lurz, Sanderson, & Rushton, 2008; Martinoli, Bertolino,  
67 Preatoni, Balduzzi, Marsan et al., 2010), and in all three countries the population of grey  
68 squirrels is still expanding (Huxley, 2003; Bosch & Lurz, 2012) and replacing red squirrels.  
69 When red squirrels in European countries are sympatric and have to compete with grey  
70 squirrels, they spend less time foraging and consume less high-energy food than their  
71 counterparts that live without the grey squirrels (Wauters, Gurnell, & Martinoli, 2001;  
72 Wauters, Tosi, & Gurnell, 2002). Measurable consequences of the competitive interactions  
73 between the species include significantly reduced red squirrel reproductive success and

74 juvenile recruitment, leading to a potentially rapid decline of the local red squirrel population  
75 (Gurnell, Wauters, Lurz, & Tosi, 2004). The red-grey squirrel system is therefore ideal for  
76 investigating whether differences in behavioural flexibility may play a part in the competitive  
77 success of the introduced species.

78

79         We first examined whether flexibility, at the outcome level, was different in the two  
80 species, using the food-extraction problem paradigm (review by Griffin & Guez, 2014).  
81 Based on invasion history in the UK (e.g. Gurnell, Lurz, & Bertoldi, 2014), we predicted that  
82 grey squirrels would be more successful and efficient than the congeneric red squirrels in  
83 solving problems. It has already been shown that grey squirrels show better spatial memory  
84 than red squirrels (Macdonald, 1997), but this may be an example of niche-specific cognition  
85 since red squirrels are less dependent on recovering scatter-hoarded caches than grey  
86 squirrels (Bosch & Lurz, 2012).

87

88         We then investigated whether flexibility, considered as a process, was a trait that  
89 predicts the differences in problem-solving performance at both between-species and within-  
90 species levels. To examine this, we followed Chow et al. (2016), by measuring such  
91 ‘flexibility’ as the rate of switching between tactics after a failed attempt (hereafter  
92 ‘instantaneous flexibility’) to solve a given problem. Across species, problem-solving  
93 performance is not always a function of instantaneous flexibility: Other traits such as  
94 persistence (rate of attempts), motor diversity (rate of emitting new types of behaviour), and  
95 selectivity (the proportion of effective behaviours emitted) have often been implicated. For  
96 example, successful problem solvers showed increased persistence (Biondi, Bo, & Vassallo,  
97 2008; Benson-Amram & Holekamp, 2012; Chow et al., 2016; Griffin et al., 2014; Van Horik  
98 & Madden, 2016) and/or high motor diversity (Benson-Amram & Holekamp, 2012; Griffin et

99 al., 2014; Griffin & Diquelou, 2015; Diquelou et al., 2016). Enhanced efficiency as a result of  
100 practice can be related to increased persistence and increased selectivity (Chow et al., 2016),  
101 or decreased motor diversity with increased experience (Griffin et al., 2014). Accordingly, we  
102 included these three behavioural traits, alongside instantaneous flexibility, when examining  
103 between- and within-species differences in problem solving.

104

105 Ideally, we would have compared red and grey squirrels living in the same habitat, to  
106 avoid any confound between environmental and species differences. However, this is not  
107 possible because once grey squirrels enter red squirrel habitats, either the number of red  
108 squirrels declines (often rapidly due to the added risk of squirrelpox virus disease  
109 transmission; Rushton, Lurz, Gurnell, & Fuller, 2000; Sainsbury, Nettleton, Gilray, &  
110 Gurnell, 2000) or the greys are removed by humans in an effort to prevent that happening (for  
111 an overview of the current removal project in Scotland, control operations and the pox issue,  
112 see <https://scottishsquirrels.org.uk/about/project-overview/>). We therefore had to study  
113 separate populations of the two species. Within the range of habitats currently occupied by  
114 red and grey squirrels in the UK, we matched our study sites as closely as we could for  
115 climate, season, vegetation types, predation risk, the number of foraging squirrels, and the  
116 level of human activity. We also used study sites as widely spread as possible within each  
117 habitat, to maximise the genetic diversity within our sample and in order to avoid sampling  
118 the same individuals from each population.

119

## 120 **METHODS**

### 121 *Ethical note*

122 Our study was approved by the Ethical Review Group at the University of Exeter (no.  
123 2012/533). Experiments were carried out in accordance with Association for the Study of

124 Animal Behaviour guidelines on animal welfare and UK law. Initially, we used trapping  
125 method to identify individuals. Between April and September, 12 traps were set at different  
126 locations in the University of Exeter campus from dawn to dusk. Traps were checked every  
127 1.5-2 hours. When a squirrel was captured, we transferred it to a mesh cylinder-shaped tube  
128 (or a handling cone). We PIT tagged and marked each squirrel with a different pattern at  
129 different body parts, using commercial hair dye. Individuals were released once they had  
130 been sexed and weighed. No deaths occurred as a result of trapping. As the trapping process  
131 appeared to deter squirrels from participating in these experiments (only 4 out of 43 trapped  
132 squirrels interacted with the test apparatus), we used the individuals' unique characteristics  
133 for identification for the rest of the experiment (see below '*Animal Identification*'). The  
134 experiments did not involve invasive methods; squirrels voluntarily approached and left the  
135 apparatus. The apparatus was placed away from roads and in locations with low risk of  
136 predation to avoid exposing the squirrels to added risk from participating in the experiments.

137

### 138 *Study habitats, study sites and study populations*

139 We collected data from two free-ranging squirrel populations in habitats that contained either  
140 grey squirrels or red squirrels exclusively. The grey squirrel habitat consisted of woodlands  
141 neighbouring the University of Exeter campus, Devon, England (50.74°N, 3.54°W), or on the  
142 campus itself. Data were collected from eight sites within this habitat, between October 2013  
143 and January 2014, and between December 2014 and February 2015. The red squirrel habitat  
144 consisted of woodlands around Brodick castle and country park (55.59°N, 5.15°W), Brodick,  
145 Isle of Arran, Scotland. Data were collected from seven sites within this habitat, from  
146 September to November 2014. All sites were public areas, were 500-800 m apart, had low  
147 predation risk, and had three to five squirrels that foraged regularly within them. Both

148 habitats had exotic trees such as Sessile oak (*Quercus petraea*), Scots Pine (*Pinus sylvestris*),  
149 beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*).

150

#### 151 *Animal identification*

152 Squirrels were identified from video recordings, using frame-by-frame analysis in the  
153 software Adobe Premiere Pro CS6. Most squirrels were identified using their unique  
154 characteristics such as coat colour, tail shape, body size, ear shape, and paw colour, as well as  
155 identifiable marks on face and body. This procedure required intensive observer training,  
156 typically around two months for each species. Four grey squirrels had been marked with  
157 black hair dye in a previous trapping effort to facilitate identification.

158

#### 159 *Apparatus and equipment*

160 We designed two problems that could both be solved within squirrels' behavioural repertoire,  
161 but which varied in their expected difficulty so that we could observe a range of problem-  
162 solving ability. Fig. 1a shows the apparatus for the easy task. It consisted of a hinged box (12  
163 x 12 x 4.5 cm, Length x Width x Height). It had four plastic wells, one at each corner (4.5 x 3  
164 x 1.5 cm), and each well was covered by a hinged transparent lid (3 x 3 cm). Fig. 1b shows  
165 the apparatus for the difficult task. It consisted of the puzzle box that had been used in a  
166 laboratory study (Chow et al., 2016). This task was expected to be more difficult than the  
167 hinged box task for the squirrels, as it required counter-intuitive methods to solve it. The  
168 apparatus consisted of a transparent Plexiglas box (25 x 25 x 19 cm), which had ten holes (2  
169 x 0.9 cm, W x H) located on each side, and a pyramid-shaped base (25 x 25 x 3 cm). The ten  
170 holes on each side of the box were horizontally but not vertically aligned with holes on the  
171 opposite side. Levers were inserted across the box through holes roughly opposite to each  
172 other. The box was secured above the base by four wooden legs so that there was a gap



173 between the box and the base, allowing a squirrel to obtain nuts when it had solved the  
174 problem. The gap for grey squirrels was 4.5 cm and for red squirrels was 3.5 cm, as red  
175 squirrels have shorter body length than grey squirrels. During the main testing, ten plastic  
176 levers were inserted through holes across the box, protruding from the box by 2.5 cm at each  
177 end. Each lever (1.5 x 29.8 x 0.5 cm; Length x Width x Thickness) had a 3-sided Plexiglas  
178 nut container (back: 2 x 1.5 cm; side: 1.5 x 1.5 cm) at one end; this was positioned just inside  
179 the box. The back of the nut container was transparent and its sides were white, so the  
180 squirrels could view the nut from two opposite sides of the box. This design allowed a  
181 squirrel to cause a lever to drop, and thereby obtain a nut if there was one in the nut  
182 container. This could be achieved by pushing the lever end that was near to the nut  
183 (henceforth, ‘near end’), or by pulling it from the opposite end (henceforth, ‘far end’). These  
184 tactics are referred to below as “effective”. However, the problem could not be solved by the  
185 more intuitively obvious tactics of pulling at the near end or pushing the far end; these tactics  
186 are referred to below as “ineffective”.

### *Figure 1*

#### 187 *Procedures*

188 Before the experiment started, an experimenter (i.e. the first author) chose a location that was  
189 away from main roads and that was covered by bushes and trees. This aimed to minimise  
190 risks to the squirrels from predation risk or vehicles. Once a suitable location was chosen, the  
191 experimenter placed hazelnuts in the shell and hazelnut kernels to attract squirrels. Baits were  
192 checked twice a day for three consecutive days before the experiment. We re-baited the sites  
193 twice a day if squirrels took the hazelnuts. In the main experiment, we set the easy task on the  
194 ground at a random position to minimise the chance of squirrels using box position as a cue  
195 to open a lid. However, squirrels could use the length and the width of the lid to indicate  
196 which side to lift. During testing, each well contained one hazel nut. Because the difficult

197 task was much larger than the hinged box, and object size has been shown to affect  
198 neophobic response (Mettke-Hoffmann, Rowe, Hayden, & Canoine, 2006) and in turn,  
199 problem-solving performance (Overington et al., 2011), we minimised any such effect for the  
200 difficult task by giving a 4-hour habituation period to squirrels (Overington et al., 2011;  
201 Webster & Lefebvre, 2001). During this period, we presented the transparent box without  
202 levers, and placed 10 shelled hazelnuts on each side of the box. All squirrels approached and  
203 explored the apparatus. While we did not observe neophobic responses to either task during  
204 the main experiment (see videos in the supplementary materials), we could not completely  
205 exclude the possibility that squirrels were still neophobic to the apparatuses when they were  
206 solving the task. The box was placed either 80 cm away from a tree or inside bushes and  
207 close to trees to minimise predation risks. The puzzle box had ten levers inserted during the  
208 main testing; five levers were baited with hazelnuts and five levers were empty (control).  
209 Squirrels were free to come and go from the box and thus the number of nuts that each  
210 individual obtained could vary between trials. To prevent squirrels from using the positions  
211 of the holes or the direction of the cover relative to the tree to solve the task, we randomised  
212 the side from which the levers were inserted, the direction of the nut containers, and which  
213 levers were baited with nuts between trials. The order of presentation of the two tasks was  
214 counter-balanced across sites.

215

216 Throughout the experiment, there were 2-4 squirrels active at each location. We took into  
217 account the individuals' varied active periods to minimise conspecific competition. We set up  
218 the apparatuses daily from dawn to dusk regardless of weather condition. We further re-  
219 baited the apparatus at one- to two-hour intervals. Accordingly, five to eight trials were  
220 carried out daily depending on the available daylight. This schedule allowed us to collect data  
221 from single individuals most of the time; fewer than 1% of attempts had two or more

222 individuals on or around the apparatus. In these situations, dominant squirrels chased  
223 subdominant squirrels away or subdominant squirrels would wait until the dominant squirrels  
224 left before approaching the apparatus. A video camera (Panasonic SWD HD-90) mounted on  
225 a tripod was placed 60 cm away from the apparatus to capture all task behaviours. During the  
226 data collection period with the grey squirrels, an experimenter (the first author) was present  
227 25 m away from the apparatus in three of the eight locations, since these squirrels were  
228 relatively habituated to humans using the university campus.

229

### 230 *Measurements*

231 To compare between-species problem-solving performance, we first divided squirrels in each  
232 species into ‘problem solvers’ and ‘non-solvers’. Problem solvers were squirrels that  
233 successfully solved the tasks repeatedly whereas non-solvers were those that never solved the  
234 tasks throughout the entire experiment, or that solved the tasks once but did not repeat that  
235 success on subsequent visits (squirrels that solved the problem more than once always went  
236 on to solve it multiple times). We then further divided problem solvers into ‘first-time  
237 solvers’ (those that solved the problems on their first visit) and ‘subsequent solvers’ (those  
238 that failed on their first visit but succeeded on a subsequent visit). A visit was recorded as  
239 starting when a squirrel was seen in the video to manipulate a lever or lid, and continued until  
240 it left the view of the video for two or more minutes. Visit durations largely reflected solving  
241 duration, but also included brief periods of visual ‘inspection’ of the apparatus. Success for  
242 the easy task was defined as a squirrel using its mouth, nose or front paw to lift up one of the  
243 four transparent lids. Success in the difficult task was defined as a squirrel using any of its  
244 body parts to manipulate a lever and causing the lever and/or a nut to drop.

245

246 To obtain detailed behavioural data about squirrels' problem-solving process, we focused on  
247 the behaviours that were exhibited during each attempt at problem solution. An attempt  
248 started when a squirrel used any of its body parts to contact a transparent lid in the easy task  
249 or a lever in the difficult task and ended when the squirrel stopped contacting that part of the  
250 apparatus. A new attempt was counted if the squirrel changed to manipulating another part of  
251 the apparatus. Attempts were counted regardless of whether the squirrel employed effective  
252 or ineffective behaviours for the task, and regardless of any switches between tactics  
253 exhibited and of the number of types of behaviour used. Recording attempts provided two  
254 measurements for each task:

255

256 *Solving duration.* We calculated each attempt duration as the time from when a squirrel used  
257 any of its body part to touch a lid/a lever to when the squirrel stopped touching the lid or  
258 lever (in the case of unsuccessful attempts) or when the squirrels opened a lid/made a lever  
259 and/or nut drop (in the case of success). The solving duration consisted of the sum of all  
260 attempt durations until a success occurred. Solving duration was our main measure of the  
261 efficiency of problem solving (i.e. how quickly a squirrel solved a task), but it was also used  
262 in our quantification of behavioural traits, as follows.

263

264 *Persistence.* Following previous authors (Biondi et al., 2008; Chow et al., 2016; Griffin et al.,  
265 2014), for each success, we obtained the total number of attempts, divided this number by the  
266 solving duration to obtain the rate of attempting to solve the problem, and used this as a  
267 measure of the behavioural trait persistence. Converting persistence to a rate allowed us to  
268 measure it independently of the inherent relationship between the number of attempts and  
269 solving duration (Chow et al., 2016). We regarded persistence as a measure of motivation for

270 problem solving (Griffin et al., 2014; Chow et al., 2016, Chow, Lea, Hempel de Ibarra, &  
271 Robert, 2017).

272

273 The difficult task allowed squirrels to exhibit different types of contact with the apparatus.

274 This enabled us to measure three further behavioural traits, namely motor diversity,

275 selectivity and instantaneous flexibility. Like persistence, motor diversity and instantaneous

276 flexibility were measured as rates (frequency of occurrence/total solving duration to success)

277 to minimise confounding with solving duration.

278

279 *Motor diversity* was measured as the rate of exhibiting different types of contact with the

280 puzzle box, using the list of types shown in Table A1 (reproduced from Table 1 of Chow et

281 al., 2016). Nine types of contact were recorded, including push up, push in, pull, tilt up, claw,

282 lick, shake and two or more of these types of behaviours occurring simultaneously (hereafter,

283 combined behaviours). Squirrels therefore received a score ranged from 1 to 9 as diversity.

284 We then divided this number by their solving duration to obtain the rate of motor diversity.

285

286 *Instantaneous flexibility* was measured as the rate of switching between tactics. Using the

287 definitions of contact types in Table A1, a switch was recorded whenever a squirrel changed

288 from one type of tactic to another type after a failed attempt. Switches were recorded

289 regardless of whether the current tactic has been previously used and regardless of whether

290 the tactic was effective or ineffective. We obtained the total number of switches across

291 attempts and divided this number by the total solving duration to obtain the rate of

292 instantaneous flexibility.

293

294 *Selectivity* was measured as the proportion of effective behaviours shown. As noted above,  
295 the effective behaviours were either pushing the ‘near-end’ or pulling the ‘far-end’ of a lever,  
296 and ineffective behaviours were either pushing the ‘far-end’ or pulling the ‘near-end’. We  
297 obtained the number of effective behaviours that a squirrel exhibited and divided this number  
298 by the total number of effective and ineffective behaviours to give our measure of selectivity.

299

### 300 *Statistical analyses*

301 For each task, we used Chi-square tests to compare the frequencies of individuals in the two  
302 species that obtained success in their first visit and success in the subsequent visits.  
303 Generalized Linear Model (GLM) was used to compare tasks’ (‘easy’ or ‘difficult’) solving  
304 duration on the first success for each species and to examine between-species (‘grey’ or ‘red’  
305 squirrels) differences in behavioural traits on the first success for the difficult task. To  
306 examine how performance varied with experience, we chose a fixed number of successes,  
307 after which little or no improvement in performance could be detected, and eliminated data  
308 from squirrels that obtained fewer successes. For the easy task, we used data from the first  
309 15 successes, and were able to include data from most of the squirrels (24 individuals, 11  
310 grey and 13 red squirrels, 75% of the total). For the difficult task, performance took longer to  
311 reach asymptote, and we used data from the first 40 successes, contributed by 18 individuals  
312 (11 grey and 7 red squirrels, 42% of the sample). In the analysis for the easy task, we used the  
313 Gamma log link function to accommodate values that were positively skewed but not  
314 massively concentrated on or close to zero for continuous variables, and the Poisson log link  
315 function for count variables. In the analysis for the difficult task, we used Generalized  
316 Estimating Equations (GEE) with exchangeable working correlation (Liang & Zeger, 1986)  
317 and Tweedie identity link function to accommodate mass values that were close to zero for  
318 continuous variables. We included species, success number and their interaction as

319 independent variables when analysing solution time across success number. GEE was also  
320 used to examine between- and within- species differences in each behavioural trait. Finally,  
321 GEE was used to examine what factors were associated with enhanced efficiency in the  
322 difficult task for each species. For this analysis, we log-transformed the solution times to  
323 normalise their distribution before applying the Gaussian distribution for model estimation.  
324 Pearson correlations were used to investigate highly correlated variables (i.e.  $r > 0.5$ ; see  
325 supplementary material Table A2). As motor diversity and persistence were highly correlated  
326 in both species ( $r = 0.74$  for red squirrels and  $r = 0.89$  for grey squirrels), we minimised  
327 confusion in interpreting the results by dropping motor diversity from the analyses. The  
328 decision to retain persistence over motor diversity was because persistence has been shown to  
329 be a key trait for this difficult task (Chow et al., 2016). Significance levels reported here are  
330 two-tailed and critical level was  $P \leq 0.05$ . We further applied Bonferroni corrections to  
331 adjust the  $P$  values for multiple comparisons at between- and within- species levels, and  
332 significance level was then set at  $P \leq 0.025$ . All data were analysed using SPSS version 23.

333

## 334 **RESULTS**

### 335 *Within-species task comparison*

336 Task was a significant factor for solution duration in grey (GLM  $\chi^2_1 = 7.81$ ,  $P = 0.005$ ) and  
337 red squirrels ( $\chi^2_1 = 9.68$ ,  $P = 0.002$ ); the solution duration in the difficult task on the first  
338 success was significantly higher than in the easy task for both species. On their first success,  
339 grey squirrels took a mean of 4.3s (SE  $\pm$  1.2s) to solve the easy task whereas they took 12.7s  
340 (SE  $\pm$  4.7s) to solve the difficult task. Red squirrels took a mean of 3.9s (SE  $\pm$  0.7s) to solve  
341 the easy task on their first success whereas they took 9.4s (SE  $\pm$  2.1s) to solve the difficult  
342 task. This confirmed that, as intended, the puzzle box was more difficult than the hinged box  
343 for the squirrels.

344

345 *Performance in the easy task*

346 14 grey squirrels and 18 red squirrels attempted the easy task. Of these squirrels, 13 (93%)  
347 grey and 9 (50%) red squirrels solved the task on their first visit. This species difference in  
348 first-time success in solving the easy task was significant (Fisher's exact test:  $P = 0.019$ ).  
349 Amongst these first-time solvers, grey squirrels spent an average of 4.2s (SE  $\pm 1.3$ s) solving  
350 the task whereas red squirrels spent an average of 1.6s (SE  $\pm 0.2$ s) to solve the task. This  
351 species difference in first-time solvers' solving duration was significant (GLM  $\chi^2_1 = 9.27$ ,  $P =$   
352  $0.002$ ). Red squirrel non-solvers spent significantly longer time manipulating the task on their  
353 first visit (Mean = 5.19s, SE  $\pm 8.8$ s) than red squirrel problem solvers ( $\chi^2_1 = 5.66$ ,  $P = 0.017$ ),  
354 but their manipulation times did not differ significantly from those of grey squirrel problem  
355 solvers ( $\chi^2_1 = 0.72$ ,  $P = 0.396$ ).

356

357 The squirrels that did not succeed on their first visit all succeeded on subsequent visits (see  
358 *Within-species task comparison* above for the mean and standard errors of the solving  
359 duration on the first success in the easy task for each species, for the 14 grey and 18 red  
360 squirrel problem solvers). Fig. 2a shows the solving duration for the 24 squirrels (11 grey and  
361 13 red) that completed 15 successes. Species did not differ in solving duration (GEE  $\chi^2_1 =$   
362  $1.40$ ,  $P = 0.237$ ). All squirrels increased their efficiency with experience of success ( $\chi^2_1 =$   
363  $18.59$ ,  $P < 0.001$ ). The interaction between species and success number was not significant  
364 ( $\chi^2_1 = 0.98$ ,  $P = 0.323$ ).

365

366 Fig. 2b shows how attempt rate, our measure of persistence, varied with experience and  
367 species. It was significantly higher in the grey squirrels than the red squirrels ( $\chi^2_1 = 4.95$ ,  $P =$   
368  $0.026$ ). Attempt rate increased with increased success number ( $\chi^2_1 = 79.44$ ,  $P < 0.001$ ). Its



369 interaction with species was also significant ( $\chi^2_1 = 10.51, P = 0.001$ ); as Fig. 2b shows, with  
 370 increased experience of success, attempt rate decreased in grey squirrels but increased in red  
 371 squirrels. These results may reflect the two species using different strategies to interact with  
 372 the task (e.g. grey squirrels may make few long-bout attempts whereas red squirrels may  
 373 make more short-bout attempts across the success number). To understand this further, we  
 374 focused on whether the two species differed in their actual number of attempts made and the  
 375 mean duration of each attempt (i.e. solving duration/the number of attempts) when solving  
 376 the easy task. Figure 2c shows the actual number of attempts made across 15 successes.  
 377 Success number had a significant main effect ( $\chi^2_1 = 21.27, P < 0.001$ ); the number of attempts  
 378 decreased across the 15 successes. Neither species ( $\chi^2_1 = 0.88, P = 0.348$ ) nor the interaction  
 379 between species and success number were significant ( $\chi^2_1 = 0.35, P = 0.851$ ). Figure 2d  
 380 shows the length of each attempt across 15 successes for each species. Species differed  
 381 significantly in the mean attempt duration across 15 successes ( $\chi^2_1 = 4.40, P = 0.036$ ); grey  
 382 squirrels made shorter attempts than red squirrels. Both species decreased the duration of  
 383 each attempt across 15 successes ( $\chi^2_1 = 19.04, P < 0.001$ ) and the interaction of species with  
 384 success number was also significant ( $\chi^2_1 = 4.64, P = 0.031$ ); across successes, red squirrels  
 385 decreased the mean duration of an attempt bout more quickly than grey squirrels.

### Figure 2

#### 386 *Performance in the difficult task*

387 All squirrels that participated in the easy task also participated in the difficult task. A further  
 388 eight grey and three red squirrels participated in the difficult task, which yielded a total  
 389 sample size of 43 (22 grey and 21 red squirrels) for this task. Fig. 3a left panel shows that  
 390 14/22 (64%) grey and 6/21 (29%) red squirrels succeeded on their first visit (first-time  
 391 solvers). The species differed significantly in the frequency of problem-solving success on  
 392 their first visit (Fisher's exact test:  $P = 0.021$ ). These first-time solvers' solving duration did

393 not differ significantly between species (GLM:  $\chi^2_1 = 1.58$ ,  $P = 0.209$ ), although grey squirrels  
 394 tended to take longer (Mean = 12.3s, SE  $\pm$  6.8s) than red squirrels (Mean = 5.7s, SE  $\pm$  2.4s)  
 395 to solve the task on their first visit. Red squirrel non-solvers' time spent on manipulating the  
 396 task on their first visit did not differ significantly from that of their conspecifics who were  
 397 first-time solvers ( $\chi^2_1 = 3.07$ ,  $P = 0.080$ ), but they spent significantly less time than grey  
 398 squirrel problem solvers ( $\chi^2_1 = 14.32$ ,  $P < 0.001$ ) on the first visit.

399

400 Fig. 3a right panel shows that 20/22 (91%) grey squirrels and 13/21 (62%) red squirrels  
 401 solved the task on either their first or a subsequent visit; the difference between these  
 402 frequencies was also significant (Fisher's exact test:  $P = 0.039$ ). Fig. 3b shows the mean  
 403 solving duration for the 11 grey and 7 red squirrels that completed 40 successes. Among  
 404 these successful problem solvers, species differed significantly in solving duration across 40  
 405 successes (GEE  $\chi^2_1 = 5.13$ ,  $P = 0.024$ ); the red squirrels were faster than the grey squirrels, in  
 406 solving the difficult task (see *Within-species task comparison* above for the mean and  
 407 standard errors of solving duration in the difficult task). Squirrels increased efficiency with  
 408 increased experience ( $\chi^2_1 = 8.34$ ,  $P = 0.004$ ). The interaction between species and success  
 409 number had no significant effect on efficiency ( $\chi^2_1 = 0.81$ ,  $P = 0.369$ ).

### Figure 3

410 *Difficult task: between-species' behavioural trait differences, solving success*

411 On the first success, squirrels showed no significant species differences in any of the  
 412 behavioural traits that we measured: rate of attempts (GLM  $\chi^2_1 = 0.45$ ,  $P = 0.504$ , 20 grey and  
 413 13 red squirrel problem solvers), switch rate ( $\chi^2_1 = 1.21$ ,  $P = 0.272$ ), proportion of effective  
 414 behaviours ( $\chi^2_1 = 0.58$ ,  $P = 0.447$ ) or rate of motor diversity ( $\chi^2_1 = 0.01$ ,  $P = 0.930$ ). For those  
 415 squirrels that achieved 40 successes (11 grey and 7 red squirrel problem solvers), the two  
 416 species differed significantly in the switch rate across these successes, our measure of

417 instantaneous flexibility (GEE:  $\chi^2_1 = 7.03$ ,  $P = 0.008$ ,  $P < 0.025$  after Bonferroni correction),  
 418 but not in rate of attempts ( $\chi^2_1 = 0.62$ ,  $P = 0.432$ ), rate of motor diversity ( $\chi^2_1 = 3.53$ ,  $P =$   
 419  $0.060$ ), or the proportion of effective behaviours ( $\chi^2_1 = 0.44$ ,  $P = 0.506$ ). Grey squirrel  
 420 problem solvers showed lower switch rates than the red squirrel problem solvers.

421

422 *Difficult task: within-species' behavioural traits and solving duration*

423 Table 1 shows the varied contribution of behavioural traits to solving duration for each  
 424 species. Grey squirrels increased efficiency was associated with a higher rate of attempts ( $P <$   
 425  $0.001$ ) and proportion of effective behaviours ( $P < 0.001$ ) whereas red squirrels enhanced  
 426 efficiency was related to a higher rate of attempts ( $P < 0.001$ ), proportion of effective  
 427 behaviours ( $P < 0.001$ ) and level of instantaneous flexibility ( $P < 0.001$ ).

*Table 1*

428 *Difficult task: within-species' behavioural traits and solving success*

429 Because almost all grey squirrels successfully solved the difficult task, within-species'  
 430 differences in traits and performance between solvers and non-solvers could only be analysed  
 431 in red squirrels. To examine the differences between problem solvers and non-solvers, we  
 432 investigated the minimal attempts that most non-solvers made. Seven out of eight non-solvers  
 433 made at least 15 attempts. Accordingly, these non-solvers, along with all subsequent solvers  
 434 ( $N=7$ ) and first-time solvers ( $N=6$ ) were included in this within-species analyses.

435

436 Solving duration was not significantly different between non-solvers and first-time solvers  
 437 ( $\chi^2_2 = 1.70$ ,  $P = 0.192$ , Fig. 4a) or between non-solvers and subsequent solvers ( $\chi^2_2 = 2.04$ ,  $P =$   
 438  $0.154$ , Fig. 4a). Fig. 4b and c show the proportion of effective behaviours and the rate of  
 439 motor diversity for the three types of solvers. Neither trait showed a significant difference  
 440 between first-time solvers and non-solvers (selectivity:  $\chi^2_2 = 1.97$ ;  $P = 0.161$ ; rate of motor

441 diversity:  $\chi^2_2 = 4.37$ ;  $P = 0.037$ , *NS* after Bonferroni correction) or between subsequent  
442 solvers and non-solvers (selectivity:  $\chi^2_2 = 4.73$ ;  $P = 0.030$ , *NS* after Bonferroni correction;  
443 rate of motor diversity:  $\chi^2_2 = 0.039$ ;  $P = 0.844$ ). Fig. 4d shows the rate of instantaneous  
444 flexibility for the three types of solvers. Non-solvers showed significantly lower switch rates  
445 than first-time solvers ( $\chi^2_1 = 13.68$ ;  $P < 0.001$ ;  $P < 0.025$  after Bonferroni correction), but  
446 their rates were not different from those of subsequent solvers ( $\chi^2_1 = 0.71$ ;  $P = 0.401$ ). We  
447 also examined the rate of producing productive switches (i.e. when squirrels switch from  
448 ineffective to effective behaviours after a failed attempt). Fig. 4e shows the rate of productive  
449 switches among the three categories of squirrel. Non-solvers showed a significantly lower  
450 rate of productive switches than first-time solvers ( $\chi^2_2 = 13.68$ ;  $P < 0.001$ ,  $P < 0.025$  after  
451 Bonferroni correction) and subsequent solvers ( $\chi^2_2 = 13.68$ ;  $P < 0.001$ ,  $P < 0.025$  after  
452 Bonferroni correction).

*Figure 4*

453 **DISCUSSION**

454 Using two food-extraction tasks, we provide the first detailed empirical study of the  
455 differences in the level of flexibility between an invasive and a native mammalian species  
456 that compete with each other. In between-species analyses, our results indicate that invasive  
457 grey squirrels have higher behavioural flexibility at the outcome level than native red  
458 squirrels. The grey squirrels were more likely than the reds to solve the easy task on their first  
459 visit, and a higher proportion of grey than red squirrels solved the difficult task. However, red  
460 squirrel problem solvers showed comparable solving duration to grey squirrel problem  
461 solvers in the easy task, and among the squirrels that did solve the difficult task, grey  
462 squirrels were less efficient than red squirrels. At within-species level, red squirrel problem  
463 solvers' increased efficiency was associated with an increase in instantaneous flexibility, and  
464 failure in problem solving was associated with low instantaneous flexibility. Together, these

465 data reveal that flexibility overlaps between the two species, but with a much wider range of  
466 problem-solving ability in the red squirrels than in the grey squirrels. Analyses of the  
467 contributions of problem-solving related behavioural traits showed that there are both  
468 similarities and differences between the two species in the problem-solving processes.

469

470         The high success rate of grey squirrels in solving the easy problem on the first visit  
471 (93%) and the difficult problem (91%) show that this invasive species has an advantage in  
472 problem solving. Grey squirrels have replaced the native red squirrels in most habitats in the  
473 UK and Ireland, and parts of northern Italy. This successful invasion might reflect inherently  
474 high (or 'superior' as it is termed in other references e.g. Elton, 1958; Sakai, Allendorf, Holt,  
475 Lodge, Molofsky et al., 2001) flexibility in grey squirrels. However, the higher problem-  
476 solving ability we observed could also be explained by selective pressure during the invasion  
477 process, if enhanced flexibility is favoured as a trait when invading a new environment  
478 (Wright, Eberhard, Hobson, Avery, & Russello, 2010). To disentangle inherent capacity from  
479 selective pressure, it would be necessary to compare the grey squirrels' problem-solving  
480 ability in a non-native environment with their problem-solving ability in their native  
481 environment in Eastern North America.

482

483         Given an easy problem, red squirrels non-solvers spent longer manipulating the task  
484 than their counterpart solvers and comparable amount of time to grey squirrels problem  
485 solvers, but still failed to solve the problem on their first visit. Given a more difficult  
486 problem, the majority of red squirrels (71%) failed to solve it on their first visit (Fig. 3a).  
487 Even though the 29% of the red squirrels that did solve the difficult task at their first visit  
488 showed comparable solving efficiency to grey squirrels, and those red squirrels that  
489 completed 40 successes came to outperform the grey squirrels with increased successes (Fig.

490 3b), these results indicate that at the population level the native red squirrels are less flexible  
491 at the outcome level than grey squirrels. Our analysis at within-species level further indicates  
492 that instantaneous flexibility, flexibility at the process level, was low among the red squirrel  
493 non-solvers. Where the two species co-exist, red squirrels' foraging efficiency is depressed  
494 (Wauters et al., 2001, 2002), but since the habitats we used only had a single species, our  
495 results could not be due to such a competitive effect. Yet, clear differences in problem-  
496 solving ability were observed. Although the habitats in which we observed the two species  
497 were not completely identical, as far as we know, none of the differences between them has  
498 been shown to correlate with differences in problem-solving performance. Accordingly, a  
499 difference in behavioural flexibility may be added to the causes that lead to the red squirrels'  
500 population decline, alongside competition for food sources (Wauters et al., 2001, 2002) and  
501 squirrelpox (Rushton, Lurz, Gurnell, & Nettleton, 2006). Problem-solving ability will be  
502 critical for both species in resource exploitation and survival, so differences in flexibility may  
503 contribute to the observed patterns of species replacement, an aspect of the situation that has  
504 been completely unexplored up to now.

505

506         The facts that all squirrels eventually solved the easy task, and that some red squirrels  
507 solved the difficult task and did so efficiently, show that problem-solving ability overlaps  
508 between the two species. Our analyses showed that the two species have both similarities and  
509 differences in problem solving. For the easy task, both red and grey squirrels showed  
510 comparable solving duration, but the two species were using different strategies to achieve  
511 efficiency; grey squirrels decreased attempt rate whereas red squirrels increased attempt rate  
512 across successes (Fig. 2b). The difference was due to grey squirrels making more, shorter  
513 attempt bouts whereas red squirrels made fewer, longer attempt bouts (Fig. 2d). For the  
514 difficult task, red and grey squirrels are similar in that in both species enhanced efficiency

515 was associated with increased persistence (the attempt rate) and selectivity (the proportion of  
516 effective behaviours). These two traits have been found to be associated with efficiency in  
517 our previous studies with captive grey squirrels solving this difficult task (Chow et al., 2016),  
518 and are similar to findings in other species, for example Indian mynas, pheasants, hyenas, and  
519 meerkats (Benson-Amram & Holekamp, 2012; Thornton & Samson, 2012; Griffin et al.,  
520 2014; Van Horik & Madden, 2016). The differences in the species' problem-solving  
521 processes lay in the effects of instantaneous flexibility. In red squirrels, but not grey squirrels,  
522 instantaneous flexibility increased efficiency among those animals that solved the problem  
523 repeatedly (Table 1). Our measure of instantaneous flexibility has been shown to be related to  
524 memory in this puzzle box (Chow et al., 2017), and ability to produce a switch from  
525 ineffective to effective tactic requires the individuals to remember the effective tactic. Given  
526 that the relationship between instantaneous flexibility and selectivity was positive for the  
527 small proportion of red squirrels that were problem solvers, but negative for the grey squirrel  
528 problem solvers (Table A2), it seems that these red squirrels, at least, have better memory for  
529 their past actions than the grey squirrel problem solvers. It follows that individual variation in  
530 problem-solving ability may be wider in red squirrels than grey squirrels.

531

532 The fact that non-solvers' failure lies in flexibility-related traits raises several  
533 questions, including whether low flexibility is correlated with other sub-optimal behavioural  
534 adjustments such as decreased foraging time and consuming low energy food, which have  
535 been observed when red squirrels cohabit with grey squirrels (Wauters et al., 2001, Wauters  
536 et al., 2002); and whether low flexibility is associated with measureable negative  
537 consequences in fitness. Although these questions remain to be investigated, inefficient  
538 foraging behaviours, including inefficient food-extraction, are predicted to decrease fitness,  
539 they necessarily reduce the chances that red squirrel juveniles would be equipped for

540 reproduction. Reduced reproductive success is a major factor for the decline of red squirrels  
541 (Gurnell et al., 2004), alongside squirrelpox (Rushton et al., 2006) and food competition  
542 (Wauters et al., 2001, Wauters et al., 2002).

543

#### 544 **Conclusion**

545       Using two food-extraction tasks, we provide evidence for differences in behavioural  
546 flexibility between an invasive mammalian and a related native species. Our results show that  
547 invasive grey squirrels are more successful than the native red squirrels in solving a difficult  
548 problem, but the few red squirrels that solved the problem outperformed their grey congeners  
549 in efficiency. These results suggest that flexibility overlaps between the two species, but with  
550 a wider range of problem-solving ability in the red squirrels than in the grey squirrels.

551 Overall, our results suggest that differences in behavioural flexibility, leading to more  
552 successful problem solving, could play a part in explaining the replacement of native red  
553 squirrels by the grey invaders.

554

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## Appendix

**Table A1.** The type of behavioural tactics that squirrels used to solve the puzzle box task.

Information is Table 1 extracted from (Chow, Lea and Leaver, 2016).

Behaviours		Definitions
Pull	Effective*	A squirrel uses its teeth to make an <u>outward</u> movement and a lever subsequently moves outside the box. This pulling behaviour must be performed on the <u>near</u> end of the nut container.
	Ineffective#	A squirrel uses its teeth to make an <u>outward</u> movement and a lever does not move out of the box. This pulling behaviour must be performed on the <i>far</i> end of the nut container.
Push	Effective*	A squirrel uses any of its body part, including nose (usually), teeth, paw or chin to make an <u>inward</u> movement of a lever and the lever subsequently moves inside the box. This pushing behaviour must be performed on the <i>near</i> end of the nut container.
	Ineffective#	A squirrel uses any of its body part, including nose (usually), mouth, teeth, paw or chin to make an <u>inward</u> movement of a lever and the lever would not move. This pushing behaviour must be performed on the <u>far</u> end of the nut container.
Push up		A squirrel uses its nose to make a push under an end of a lever.
Push down		A squirrel puts force on a lever end with its paws or teeth. This behaviour makes the lever appear in a curved shape.
Tilted up		A squirrel uses its nose to level up a lever end. This behaviour makes a lever turn 45 degrees.
Claw		A squirrel uses its front paws to scratch a lever end.
Lick		A squirrel uses its tongue to touch a lever end.
Shake		A squirrel uses its teeth to bite a lever end causing an up-and-down movement.
Combined behaviours		At least two of the behavioural types that mentioned above appear.

\* indicated as direct effective contact types.

# indicated as non-effective contact types.

**Table A2.** Pearson correlations between traits within each species. Correlations at the top part are for grey squirrel problem solvers ( $N=11$ ) whereas correlations at the lower part are for red squirrel problem solvers ( $N=7$ ).

	Success number	Persistence	Selectivity	Instantaneous flexibility	Motor diversity
Success number	-	-0.01	0.17	0.07	0.01
Persistence	0.10	-	0.36	0.27	0.89
Selectivity	0.43	0.28	-	-0.06	0.34
Instantaneous flexibility	0.12	-0.07	0.09	-	0.62
Motor diversity	0.14	0.74	0.24	0.04	-

561 **Figure captions**

562 **Figure 1.** a) an easy task: a hinged box that is constructed with four containers, one at each  
 563 corner. Squirrels could lift up a lid using their front paw, nose or teeth to obtain a hazelnut. b)  
 564 a difficult task: the puzzle box that has been used in Chow et al. (2016). It is a transparent  
 565 box, constructed with 10 holes that are randomly located on each side. Squirrels could solve  
 566 the task by pushing the near-end (close to the reward) or pulling the far-end (far from the  
 567 reward).

568 **Figure 2.** Easy task: across 15 successes, 24 squirrels' ( $N_{\text{grey}} = 11$ ,  $N_{\text{red}} = 13$ ) a) mean solving  
 569 duration; b) mean attempt rate; c) mean number of attempts; and d) mean length per attempt  
 570 (i.e. attempt duration) in seconds.

571 **Figure 3.** Difficult task: percentage of problem solvers obtained first success in each species  
 572 ( $N_{\text{grey}} = 22$ ,  $N_{\text{red}} = 21$ ) on their first visit (left panel) and either on the first or at a subsequent  
 573 visit (right panel). The number above each bar indicates the actual number of squirrels that  
 574 successfully solved the task.  $*P < 0.05$ . b) mean solving duration in seconds for 18 individuals  
 575 that had completed 40 successes ( $N_{\text{grey}} = 11$ ,  $N_{\text{red}} = 7$ ).

576 **Figure 4.** Within-species analysis: box plot of each behavioural trait for non-solvers ( $N = 7$ ),  
 577 subsequent solvers ( $N = 7$ ) and first-time solvers ( $N = 6$ ). Whiskers of a box indicate  
 578 minimum and maximum values, edges of the box indicate first and third quartiles and the  
 579 internal line of the box indicates median. a) solving duration; b) selectivity, the proportion of  
 580 effective behaviour; c) motor diversity, the rate of exhibiting different types of behaviours; d)  
 581 instantaneous flexibility, the rate of switching between tactics after a failed attempt,  
 582 regardless whether the tactic has been previously used; e) productive switch, the rate of  
 583 switching from ineffective to effective tactics.  $* < 0.05$ ,  $** < 0.01$ ,  $*** < 0.001$

Figure 1

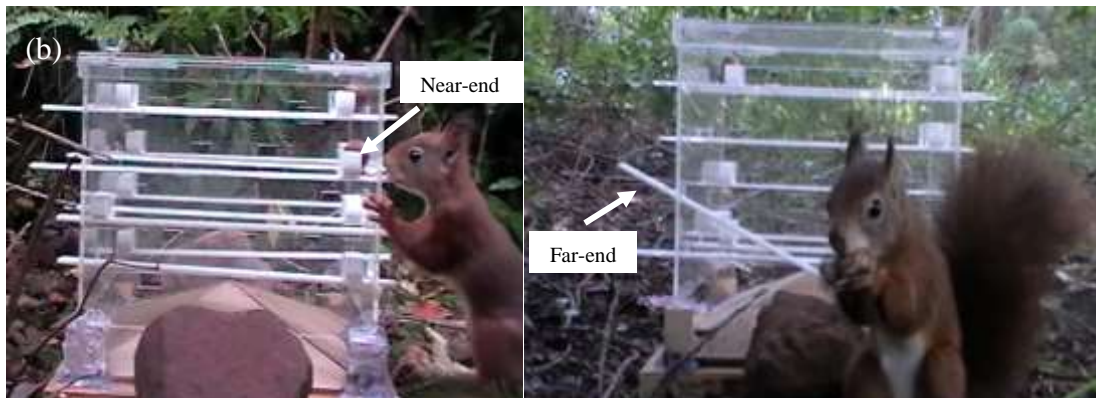
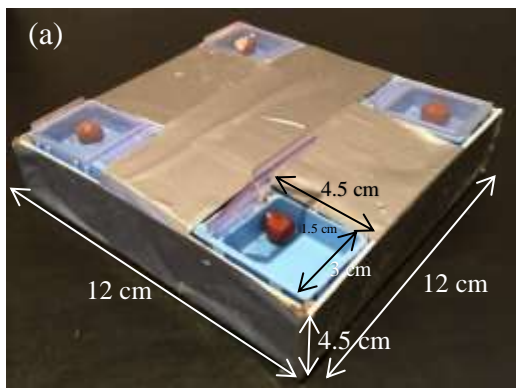




Figure 2

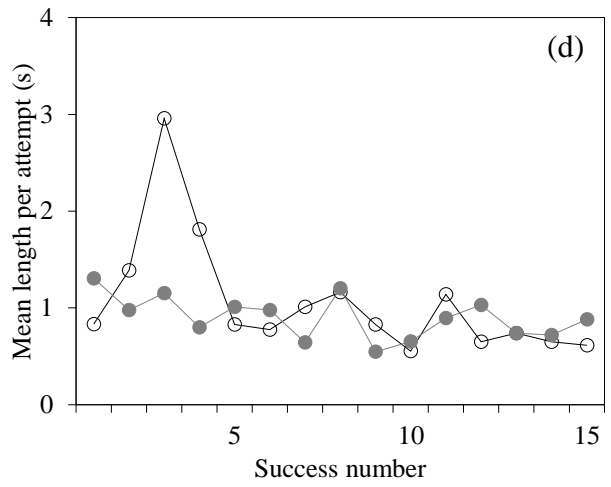
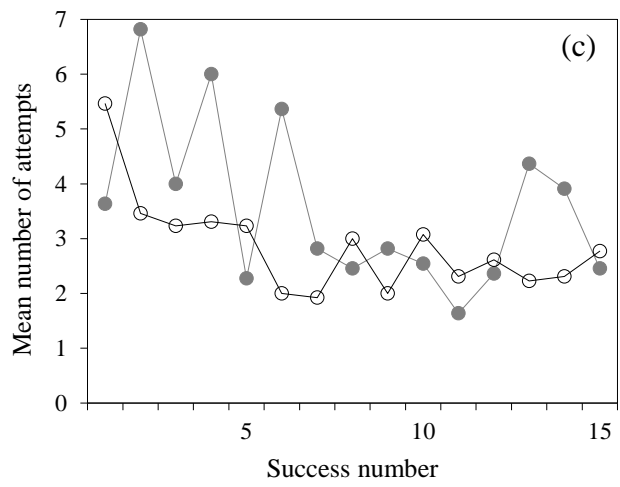
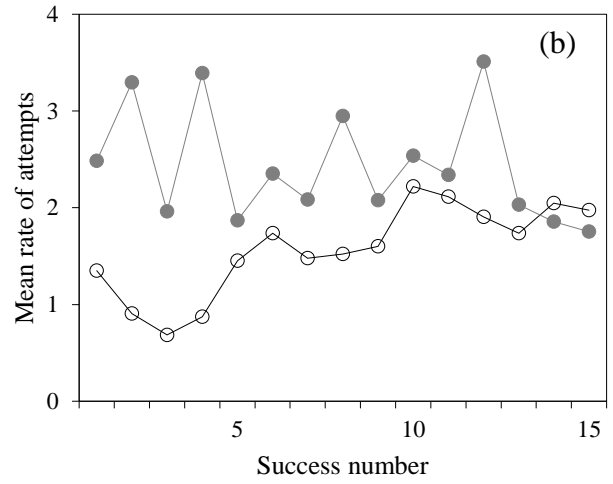
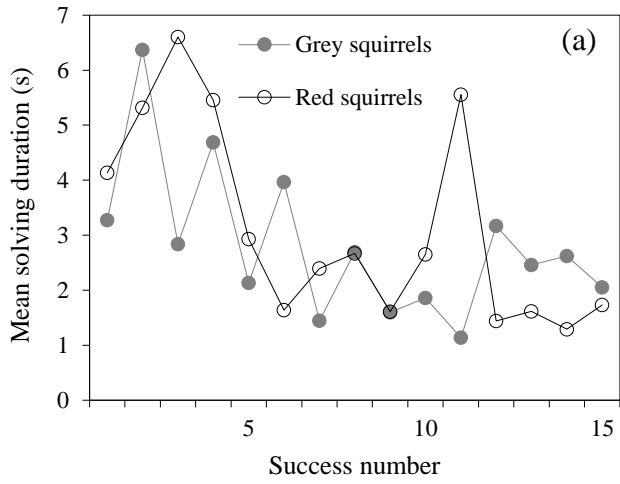


Figure 3

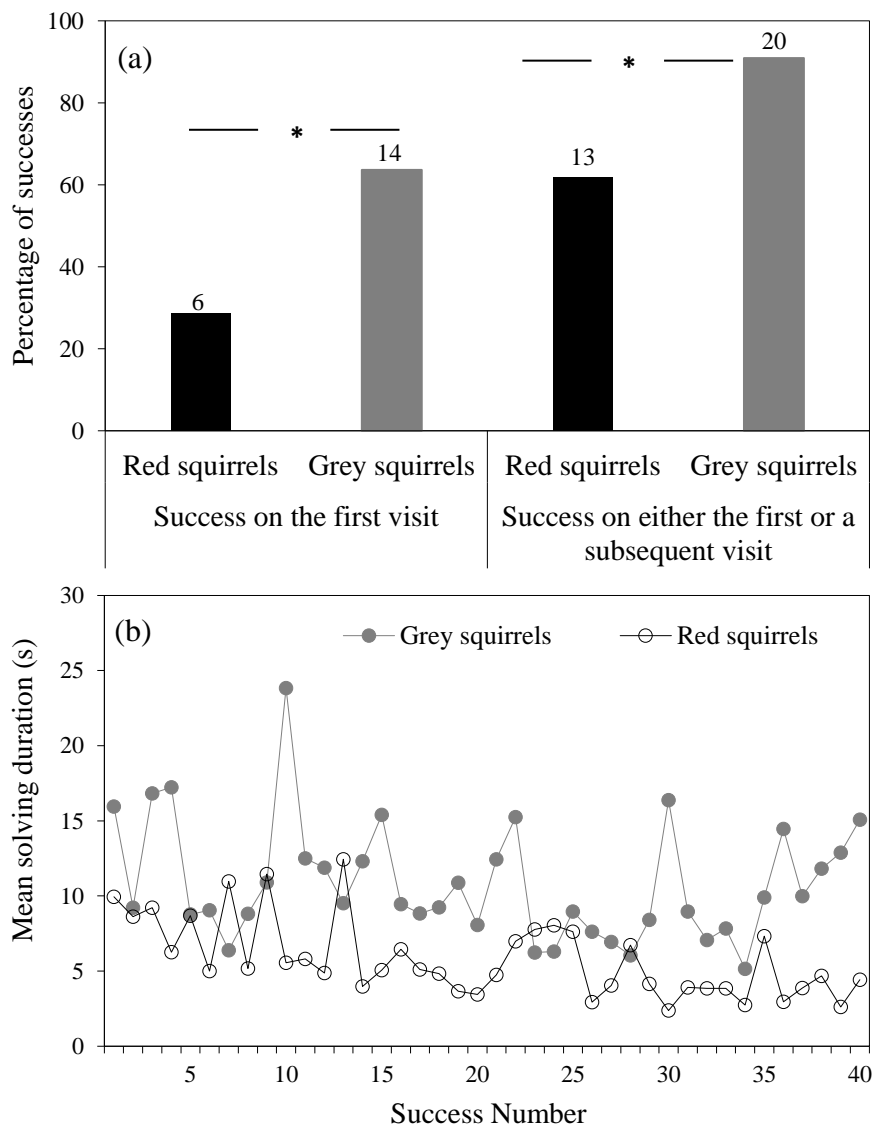
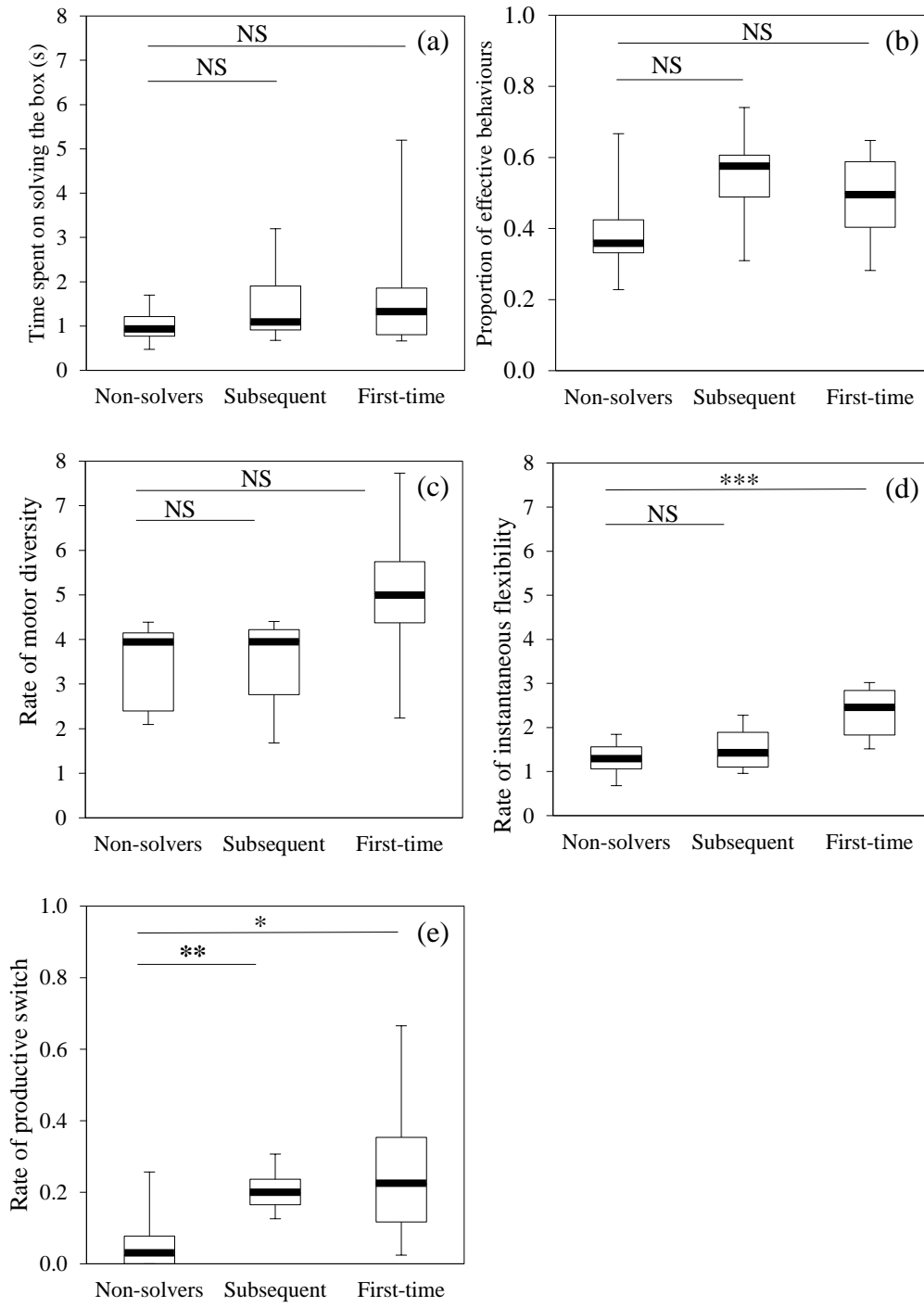


Figure 4



**Table 1.** Puzzle box task: GEE models examining the varied contribution of behavioural traits to problem-solving efficiency for each species ( $N_{\text{grey}} = 11$ ,  $N_{\text{red}} = 7$ ).

<i>40 successes</i>						
Species	Independent variable	Estimates	SE	<i>df</i>	$\chi^2$	P
Grey squirrels ( $N=11$ )	Success number	<0.01	<0.01	1	3.38	0.066
	Persistence	-0.10	0.01	1	95.78	< <b>0.001</b>
	Selectivity	-1.08	0.12	1	81.04	< <b>0.001</b>
	Instantaneous flexibility	-0.01	0.02	1	0.21	0.644
Red squirrels ( $N=7$ )	Success number	<-0.01	>0.01	1	1.60	0.206
	Persistence	-0.09	0.01	1	317.47	< <b>0.001</b>
	Selectivity	-0.37	0.11	1	11.09	<b>0.001</b>
	Instantaneous flexibility	-0.05	0.01	1	34.32	< <b>0.001</b>

Note: Factors include success number (40 trials), persistence (rate of attempts), selectivity (proportion of effective behaviours), and instantaneous flexibility (rate of switching between tactics). The table includes estimates, SE, *df*,  $\chi^2$  and P values.