

# 1 **Social influences on delayed gratification in New Caledonian** 2 **crows and Eurasian jays**

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24

## 25 **Abstract**

26

27 Self-control underlies goal-directed behaviour in humans and other animals. Delayed gratification - a  
28 measure of self-control - requires the ability to tolerate a delay and/or invest more effort to obtain a reward  
29 of higher value over one of lower value, such as food or mates. Social context, in particular, the presence  
30 of competitors, may influence delayed gratification. We adapted the ‘rotating-tray’ paradigm, where  
31 subjects need to forgo an immediate, lower-quality (i.e. less preferred) reward for a delayed, higher-quality  
32 (i.e. more preferred) one, to test social influences on delayed gratification in two corvid species: New  
33 Caledonian crows and Eurasian jays. We compared choices for immediate vs. delayed rewards while alone,  
34 in the presence of a competitive conspecific and in the presence of a non-competitive conspecific. We found  
35 that species differed: jays were more likely to select the immediate, less preferred reward than the crows.  
36 We also found that jays were more likely to select the immediate, less preferred reward when a competitor  
37 or non-competitor was present than when alone, or when a competitor was present compared to a non-  
38 competitor, while the crows selected the delayed, highly preferred reward irrespective of social presence.  
39 We discuss our findings in relation to species differences in socio-ecological factors (adult sociality and  
40 food caching) and wider implications of social influences on self-control.

41

## 42 **Introduction**

43

44 Self-control underlies decision-making and future planning, ensuring individuals are able to perform goal-  
45 directed behaviours. This process is important for humans and other animals [1, 2]. Self-control is  
46 influenced by socio-environmental factors in humans. For instance, it correlates with behavioural  
47 problems like substance abuse [3], and with measures of success, like social and academic competence  
48 [4]. It is also influenced by socio-environmental factors in other animals, such as sociality [5]. One

49 measure of self-control is the ability to delay gratification, i.e. to tolerate a delay and/or invest more effort  
50 to obtain a reward of higher value over one of lower value, such as food or mates [6]. It has been tested  
51 comprehensively using various paradigms in many species, including primates and birds [7-13]. For  
52 instance, in the exchange paradigm, subjects may choose to swap rewards with a conspecific or  
53 experimenter for a more preferred reward [14].

54 However, the role of social context on self-control is still relatively unexplored. In humans, the  
55 presence and behaviour of others can influence our own decisions [15]. For example, children engage  
56 higher cognitive control when competing or cooperating with another person [16] and are less likely to  
57 delay gratification when the experimenter behaves in an unreliable/ untrustworthy manner [17].  
58 Flexibility in self-control is likely to be important in a social context in non-human animals too, for  
59 instance, refraining from approaching food or a potential mate while in the presence of a competitor [18,  
60 19]. There are few delayed gratification studies that require interaction and co-operation with a  
61 conspecific, mostly using the token-exchange paradigm in primates [20, 21]. For example, high-ranking  
62 capuchin monkeys quickly acquired token exchange behaviour in social contexts, though low-ranking  
63 ones did not display this behavior [22]. There is therefore scope for developing tasks that explore the  
64 influence of social context and the behaviour of others on self-control.

65 Corvids (members of the crow family) have been found to differ in their ability to delay gratification  
66 [10, 23] and in sociality - living in a variety of different social systems [24]. For example, some corvids,  
67 such as Eurasian jays (E jays: *Garrulus glandarius*), are most often found alone or within a (socially)  
68 monogamous pair, who fiercely protect their own individual territories [24]. At the other extreme are the  
69 highly social corvids, such as rooks (*Corvus frugilegus*) and Western jackdaws (*Coloeus monedula*), who  
70 form large aggregations of up to 60,000 individuals [24], in which there can be a strong social hierarchy  
71 and colonial breeding [25]. Other species, such as New Caledonian crows (NC crows: *Corvus*  
72 *moneduloides*), common ravens (*Corvus corax*) and carrion crows (*Corvus corone*), show more flexibility  
73 in their sociality depending on season and age [26]. They sometimes remain within mating pairs or

74 otherwise form larger family groups with overlapping territories and even showing some instances of  
75 cooperative breeding [24].

76 Studies suggest that corvids possess complex cognitive abilities, such as the ability to plan for the  
77 future [27, 28], mentally represent problems [29, 30], make inferences [31-33], and learn abstract  
78 information [34, 35]. In the social domain, corvids show evidence for co-operative behaviors [36]; [37,  
79 38] and seem to be aware of what other individuals can see and flexibly adjust their behaviour in  
80 response. For example, ravens differentiate between knowledgeable and ignorant conspecifics [39] even  
81 after controlling for observable behavioural cues [19, 40]. Furthermore, Western scrub jays (*Aphelocoma*  
82 *californica*) re-cache their food if they have been observed by a potential pilferer during caching, but not  
83 after caching in private [41] or when observed by their mate [42]. Importantly, this re-caching only occurs  
84 when the caching jays have themselves had experience of pilfering other individuals' caches [41].

85 Western scrub jays (*Aphelocoma californica*) are able to keep track of which birds were watching  
86 them during caching, as they only defend caches against subordinates and are tolerant to their partner  
87 sharing food [42]. Like scrub-jays, Eurasian jays have also demonstrated the use and flexible deployment  
88 of various cache-protection strategies [43-46] (although see [47]). Jays cached more behind an occluder  
89 [43] and at a distance [44] when observed by a conspecific than when alone, preferentially cached less in  
90 a 'noisy' substrate when a conspecific could hear but not see them (but not when they could hear and see  
91 them) [45].

92 Furthermore, there is variation across species in the socio-cognitive abilities of corvids. Some  
93 evidence suggests that these abilities vary with the species' natural sociality. For example, when  
94 comparing highly social pinyon jays (*Gymnorhinus cyanocephalus*) with less social Western scrub-jays  
95 on two complex tasks related to tracking and assessing social relationships, the pinyon jays learned more  
96 rapidly and were significantly more accurate than the scrub jays [48]. Additionally, the ability to  
97 remember the locations of conspecific made caches (observation spatial memory) in order to steal them  
98 later, seems to vary in line with a species' sociality, with social Mexican jays (*Aphelocoma ultramarina*)  
99 out-performing less social Clark's nutcrackers (*Nucifraga columbiana*) [49].

100        However, Clark's nutcrackers, considered to be relatively solitary in the wild, are also able to perform  
101 a variety of cache protection strategies in the presence of a conspecific [50]. Moreover, other recent  
102 evidence suggests that variation in observational spatial memory is more related to a species' dependence  
103 on caches than their degree of sociality, as less social but frequent-caching ravens performed above  
104 chance levels in an observational spatial memory task, whereas highly social but rarely-caching jackdaws  
105 did not [51]. Therefore, the degree to which a corvids' social system influences their socio-cognitive  
106 abilities remains unclear. That said, recent research investigating the behavioral flexibility of (highly  
107 social) pinyon jays and (less social) Clark's nutcrackers under different social contexts, in which subjects  
108 were tested on their caching strategies whilst alone, observed by a conspecific, or observed by a  
109 heterospecific, suggests that each species use different cache protection behaviors. These behaviors seem  
110 to be elicited by different social cues, which can be explained in relation to the species' social  
111 organization [52]. However, very few studies have explored delayed gratification abilities in a social  
112 context, particularly in taxa that differ in sociality.

113        We aimed to test the flexibility of delayed gratification in a social context in two corvid species -  
114 New Caledonian crows (NC crows) and Eurasian jays (E jays) - exploring their choices for immediate vs  
115 delayed rewards (varying in quality and preference) while alone compared with in the presence of  
116 conspecific(s). We selected these two species as they differ in adult sociality, as outlined above, and they  
117 also differ in intensity with which they cache food (NC crows: moderate; E jays: specialized cachers) [24,  
118 53]. Furthermore, both species have been found to be able to delay gratification in previous studies,  
119 though not tested comparatively with the same paradigm or in a social context. Schnell et al [54] found  
120 that delay of gratification correlated with measures of general intelligence in Eurasian jays. Miller et al  
121 [55] found that New Caledonian crows are better able to delay gratification when rewards varied in  
122 quality over quantity and struggled when rewards (immediate or delayed) were not visible compared with  
123 being visible.

124        We used an adapted automatic rotating tray delayed gratification paradigm first introduced in a  
125 capuchin (*Cebus apella*) study by Bramlett et al. [56], which we have used previously to test New

126 Caledonian crows and young children by Miller et al. [55], where subjects were required to choose  
127 between an immediate reward or wait for a delayed one. The advantage of this paradigm is that it requires  
128 minimal pre-training (compared to exchange paradigm), does not require interaction with an experimenter  
129 and can be run effectively comparatively. While the rotating tray paradigm has not been used in Eurasian  
130 jays previously, this species has been tested using other delay of gratification paradigms (inter-temporal  
131 delay maintenance task: Schnell et al., [54]). We used a within-subject, repeated measures design and  
132 rewards that differed in quality.

133 We tested whether corvids can flexibly alter their decision as to whether to wait for a better reward in  
134 response to current social conditions, specifically, whilst alone, in a competitive situation (e.g. dominant  
135 conspecific), vs a non/less competitive one (subordinate conspecific). We compared behavioural choices  
136 between conditions on the individual and species level, and where possible, compared performance  
137 between species. Based on our hypothesis that delayed gratification will vary under different social  
138 contexts, we predicted that both species may alter their behaviour in the presence of a conspecific  
139 compared to being alone, particularly when the conspecific was a competitor. We expected that the birds  
140 may wait for the higher-quality (i.e. more preferred) reward when alone (as in Miller et al., [55]) and  
141 potentially with a non-competitor conspecific, but may choose the lower-quality, immediate reward (even  
142 though less preferred) when a competitor was present (Table 1), as waiting would risk losing the reward  
143 to a competitor, leaving the focal bird with nothing.

144

145 **Table 1. Predicted selections by condition (social context)**

<b>Condition</b>	<b>Prediction for test trial selection</b>
Alone (i.e. baseline)	Delayed; higher-quality reward
Non/less-competitor	Delayed; higher-quality reward (may vary by species)

Competitor	Immediate; higher or lower-quality reward
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146

## 147 **Materials and Methods**

148

### 149 **Subjects**

150

#### 151 **New Caledonian crows**

152 Eleven New Caledonian crows (NC crows) were caught from the wild (at location 21.67°S 165.68°E) on  
153 Grand Terre, New Caledonia, for temporary holding in captivity on the Island for non-invasive behavioural  
154 research purposes from April to August 2019, of which six were available for inclusion in this study. The  
155 other five birds were not available as they were engaged in other parallel experiments at the field site, with  
156 data collection period limited by season length and experimenter availability. There were three males and  
157 three females, based on sexual size dimorphism [57], of which one was adult, two were in their second year  
158 (not breeding, remaining in their family group) and three were juveniles (less than 1 year old) (S1 Table).  
159 The birds were identifiable with leg-rings. During the field season, all crows took part in several  
160 experiments, including making forced 2-choices (e.g. between 2 tools or food types) and interacting with  
161 artificial apparatuses (e.g. [55]). The birds were housed in a ten-compartment outside aviary, with  
162 compartments differing in size, though all at least 2 x 3 x 3m, containing a range of natural enrichment  
163 materials like logs, branches and pinecones. Subjects were tested individually in temporary visual isolation  
164 from the group, while willingly participating in the study for food rewards to enhance their motivation. The  
165 birds were not food deprived and their daily diet consisted of meat, dog food, and fruit, with water available  
166 *ad libitum*. The birds maintained at or above capture weights during their stay in captivity. The birds were  
167 acclimatized to the aviaries in April and habituated to the experimental apparatus in May, completing the  
168 study in August 2019. At the end of their research participation, birds were released at their capture sites.

169 Hunt [58] indicated that New Caledonian crows housed temporarily in a similar situation as the present  
170 study successfully reintegrated into the wild after release.

171

## 172 **Eurasian jays**

173 Eight Eurasian jays (E jays; four males; four females; all adults: S1 Table) participated in this study from  
174 September 2022 to May 2023, of which five jays reached criterion for testing. All jays were hand-reared at  
175 10 days old from wild eggs collected by a registered breeder under a Natural England License to NSC  
176 (20140062) in 2015. The jays were housed together within a large outdoor aviary (20 m long  $\times$  10 m wide  
177  $\times$  3 m high) at the Sub-Department of Animal Behaviour, University of Cambridge, Madingley,  
178 Cambridgeshire, UK. One end of the aviary was divided into smaller subsections (6  $\times$  2  $\times$  3 m), used to  
179 separate mate pairs during the breeding season. Hatch doors connected these subsections to separate indoor  
180 testing compartments (each 2 x 1 x 2 m) and could be opened or closed to isolate individuals. Subjects were  
181 identified using unique leg-ring color combinations. The jays had *ad libitum* access to water (including  
182 during testing) and were fed a mixture of soaked dog or cat biscuits, boiled eggs, boiled vegetables, seeds,  
183 and fruit, twice a day. During test days, this food was removed from the aviary approximately 1 hour before  
184 testing to increase the jays' motivation to come inside the testing compartments and to participate in  
185 experimental trials. The birds were only food restricted for a maximum of 4 hours in one day, although as  
186 they habitually cache food, they may have had access to non-test foods during this time. All subjects  
187 participated on a voluntary basis (to maximize motivation) and were separated from the group once they  
188 entered the testing compartment (by closing the hatch door). When interacting with the birds, the  
189 experimenter stood by a window in one of the test compartments.

190

## 191 **Materials**

192

## 193 **Apparatus**



194 The main apparatus used in this experiment was the same as that deployed in Miller et al., [55]. This  
195 consisted of a 38 cm diameter raised disk, fitted on top of a rotation device (moving at a speed of 68 s per  
196 revolution) which was operated using a remote control (Fig. 1). The rotating disk was enclosed within a  
197 transparent Perspex box (41 cm × 34 cm × 14 cm) with a rectangular opening at one side (29 cm × 7 cm),  
198 to prevent the birds from accessing the rewards until they were positioned directly in front of the subjects.  
199 Two small upturned, transparent plastic cups (with a string attached to facilitate cup flipping) covered the  
200 rewards and were positioned at two standardized locations on the disk, so that the first reward reached the  
201 subject after 5 s (the immediate reward), whereas the second reward reached the subject after 15 s (the  
202 delayed reward). Both cups were baited simultaneously. To standardize the position of the birds at the  
203 beginning of the trial, the tray was only started once the bird moved to be in front of the tray. The bird made  
204 a choice by touching the cup and flipping it to access the reward. Once contact was made with either of the  
205 cups, the rotating tray was stopped, meaning they were only allowed to make one choice.

206

## 207 **Procedure**

208

### 209 **Pretraining**

210 **Habituation.** To habituate the birds to the apparatus, they were gradually exposed to the apparatus in  
211 multiple phases; progressing each phase when they began taking food comfortably. First, the tray remained  
212 turned off (and so not moving) with the food placed near it. Then, the apparatus was switched on (moving)  
213 with food again placed near it. Next, the food was placed on top of the moving tray. Finally, the food was  
214 placed on top of the moving tray and the experimenter turned the tray off and on again (after each piece of  
215 food was collected) to habituate the birds to the sound the tray makes when stopping and to tray movement.  
216 Each phase was done as a group (with each individual free to leave the compartment) and then subsequently  
217 as an individual (separated from the group within the compartment).

218

219 **Food preference.** Before the main training stage, the relative preference for each food type was established  
220 per individual. To do this, both food types (high-quality: meat, low-quality: apple for NC crows; and high-  
221 quality: mealworm, low-quality: bread for E jays) were presented simultaneously in front of each subject  
222 (individually isolated in the test compartment). The bird was then allowed to choose one reward and was  
223 subsequently prevented from obtaining the other food item. This was repeated for 10 trials per session until  
224 the bird reached the criterion of choosing the high-quality reward 17/20 times (in two consecutive sessions).  
225 The position (right or left) of the high-quality reward was pseudorandomized so that it was not in the same  
226 location more than twice in a row. If a bird did not pass the criterion within 10 sessions, they were excluded  
227 from the experiment. However, all six NC crows passed within 2 sessions, and all five E jays passed within  
228 7 sessions (ranging from 2-7).

229  
230 **Forced Choice Training.** For the birds to learn that they could only make one choice of food (causing the  
231 tray to stop) in each trial, they were given trials in which only one cup was baited and the other remained  
232 empty. As such, if the food was in the delayed position, and the bird selected the immediate cup, then they  
233 did not receive a reward. In one session of 10 trials, the rewarded cup was placed at the immediate location  
234 5 times and at the delayed location 5 times, in a pseudorandomized order (so that the reward was not in the  
235 same location more than twice consecutively). The birds passed criterion for this phase when they chose  
236 the food in the delayed position in 9/10 trials across two consecutive sessions (18/20 in total). If they failed  
237 to pass this criterion within 15 sessions (i.e., 150 trials) then they were discounted from the experiment.  
238 However, all six NC crows passed within 2 sessions, and all eight E jays passed within 14 sessions (ranging  
239 from 6-14).

240  
241 **Food monopolization.** Before being tested in the test conditions, food monopolization tests were conducted  
242 to assess the relative dominance of each individual to inform the assignment of non-focal birds  
243 (competitor/non-competitor) in these trials (S1 & S2 Tables). This was always done between two  
244 individuals isolated from the rest of the group. Choices of which birds to test as non-focal birds were

245 informed by general observations of displacement and other competitive behaviors under non-test  
246 conditions. As we tested relative dominance, a single individual could be both a competitor and a non-  
247 competitor observer depending on the identity of the focal bird that they were paired with. To confirm the  
248 dominance ranking within the pair in food monopolization trials, the experimenter baited a cup on a  
249 platform whilst both birds observed, then simultaneously allowed both birds access to the baited cup. If the  
250 focal bird took the food without being displaced, then the non-focal bird was considered to be a non-  
251 competitor, but if the focal bird was displaced or did not attempt to obtain the food, then the non-focal bird  
252 was considered to be a competitor. Food monopolization trials were sometimes repeated (for the jays)  
253 immediately before test trials if observations suggested that the dominance hierarchy may have changed  
254 and non-focal birds re/assigned accordingly.

255

## 256 **Testing**

257 Upon successful completion of the forced choice phase and food monopolization trials, the birds began the  
258 test phase. This phase was made up of trials in three different conditions: ‘alone’, ‘non-competitor’, and  
259 ‘competitor’. Each bird received 2 sessions per test condition (totaling to 20 trials each). In each session,  
260 8/10 trials were ‘test’ trials (in which the high-quality reward was in the delayed position, and the low-  
261 quality reward was in the immediate position) and the remaining 2/10 trials were ‘control’ trials (in which  
262 the high-quality reward was in the immediate position, and the low-quality reward was in the delayed  
263 position). Each individual received both alone sessions first, then the remaining two social conditions. The  
264 order in which the birds received the non-competitor and competitor sessions was counterbalanced across  
265 individuals. The conditions were then alternated every session for each bird (e.g., non-competitor,  
266 competitor, non-competitor, competitor). A choice was made once the bird touched either cup and were  
267 recorded as an immediate choice (Fig. 1. a-c,; S4 Resource a), a delayed choice (i-iii; S4 Resource b), or  
268 no choice (as the non-focal bird took either reward before the focal bird could or displaced the focal bird;  
269 no choices = competitor trials:  $n = 19$ , non-competitor trials:  $n = 1$ ; S4 Resource 4c).

270

271 **Figure 1. Diagram representing the potential choices the focal bird could make in test trials. (a-c),**  
272 choosing the immediate option (less-preferred choice); **(i-iii)**, choosing the delayed option (more preferred  
273 choice). **a) / i)**, Focal bird observes as the rotating tray is bated with both food types (at an equal distance  
274 from them) while the competitor observer bird remains in an adjacent compartment with the conjoining  
275 door shut. **b)** Just before the first option becomes available, the door between the compartments is opened,  
276 allowing the non-focal bird access to the rotating tray. The focal bird then can either choose the immediate  
277 option **(c)** or ignore it as it passes **(ii)** and choose the delayed option once it becomes available **(iii)**.

278

279 **Alone.** The birds first received alone trials to assess their baseline ability to delay gratification in a non-  
280 social context, as in these trials the bird was alone in the testing compartments. The six NC crows selected  
281 the high-quality reward in the 13/16 test choices within 2 sessions (S3 Table). However, the E jays required  
282 additional training to successfully complete these baseline trials, therefore E jays' sessions were repeated  
283 until an individual made 13/16 test choices (high-quality reward was at the delayed position) to the delayed  
284 reward in two consecutive sessions. These last two sessions were then used as the alone test condition.  
285 However, if the E jays did not reach this criterion in 15 sessions, they were excluded from the experiment.  
286 Five (three females; two males) of eight jays met this criterion (ranging from 3-8 sessions). We calculated  
287 'learning speed' based on the number of trials to reach criterion in the alone condition (S3 Table).

288

289 **Non-competitor.** In these trials, the focal birds were tested with a non-competitor conspecific (determined  
290 by the food monopolization trials – see earlier) in an adjacent compartment. The non-focal bird was allowed  
291 access to the main test compartment (with the apparatus) just before the immediate reward became  
292 accessible (Fig. 1). A trial was terminated once the focal bird made a choice.

293

294 **Competitor.** In these trials, the focal birds were tested with a conspecific competitor (determined by the  
295 food monopolization trials) in an adjacent compartment. The non-focal bird was allowed access to the main

296 test compartment (with the apparatus) just before the immediate reward became accessible (Fig. 1). A trial  
297 was terminated once the focal bird made a choice or was displaced by the non-focal bird (no choice).

298

## 299 **Data Analysis**

300 We recorded the choice per trial for each subject as ‘immediate’ (1) or ‘no choice/ delayed’ (0), with  
301 proportion over total number of trials (control and test trials). All test sessions were coded live as well as  
302 being video recorded. Example trials can be found in S4 Table.

303 We conducted Linear Mixed Models (LMM: [59] with binomial distribution using R (version  
304 2023.03.0+386, [60]) to assess which factors influenced choices in the New Caledonian crows and Eurasian  
305 jays. Choice was a binary variable indicating whether the subject selected immediate (1) or delayed/ no  
306 reward (0) per trial and was entered as a dependent variable in the model. For the model, we included the  
307 random effect of subject ID and fixed effects of species (NC crows, E jays), condition (alone, competitor,  
308 non-competitor), with interaction effects of species\*condition. We used the test trial data (high-quality  
309 reward in delayed position; low-quality reward in immediate position). In control trials, all subjects selected  
310 the immediate, high-quality reward irrespective of condition (100% of trials). We used Tukey comparisons  
311 for post-hoc comparisons (package multcomp, function dlht ()) and the DHARMA package [61] to test  
312 model assumptions. The model did not fail to converge, with a confidence interval of 97.5%. Model  
313 assumption checks showed no deviation from expected distribution. For individual-level analysis, we used  
314 exact two-tailed Binomial tests of choices (delayed) per condition (SPSS version 28).

315

## 316 **Results**

317

### 318 **Group-level performance: Testing effects of condition and species**

319

320 At the group level, selection of the low-quality, immediate option differed between species (LLM:  $\chi^2 =$   
321 168.75, d.f = 2,  $p < 0.0001$ ), by condition ( $\chi^2 = 52.49$ , d.f = 1,  $p < 0.0001$ ) and within condition by species  
322 interaction ( $\chi^2 = 60.36$ , d.f = 2,  $p < 0.0001$ ). The jays were more likely to select the low-quality, immediate  
323 reward than the crows (Tukey contrasts: E jays - NC crows,  $z = 2.66$ ,  $p = 0.00782$ ). The jays were also more  
324 likely to select the low-quality, immediate reward when they were with a non-competitor than when alone  
325 ( $z = 2.676$ ,  $p = 0.00745$ ), but the difference was stronger when a competitor was present than when they  
326 were alone (Tukey contrasts:  $z = 7.270$ ,  $p < 0.0001$ ), as well as with a competitor than a non-competitor ( $z$   
327  $= -4.616$ ,  $p < 0.0001$ : Fig. 2). The crows were not more likely to select the low-quality, immediate reward  
328 depending on condition, i.e. they selected the delayed, high-quality reward irrespective of condition (Tukey  
329 contrasts: alone - competitor,  $z = -0.196$ ,  $p = 0.845$ ; alone - noncompetitor,  $z = -1.040$ ,  $p = 0.298$ ; noncompetitor  
330 vs competitor,  $z = -0.864$ ,  $p = 0.388$ ).

331  
332 **Figure 2. Proportion of choices of the immediate (low quality) reward per condition for Eurasian jays**  
333 **(EJ) and New Caledonian crows (NCC).** \*\*  $p > 0.01$ ; \*\*\*  $p > 0.001$ .

## 335 **Individual-level performance: selection of high-quality, delayed** 336 **reward by condition**

337  
338 On an individual level, all six NC crows selected the high-quality, delayed reward over the low-quality,  
339 immediate reward in all three conditions (Table 2). In contrast, while all five E jays selected the high-  
340 quality, delayed reward while alone, no jays significantly chose the delayed reward while a competitor or  
341 non-competitor was present. Rather, the E jays changed their behaviour by selecting the low-quality,  
342 immediate reward in some trials (Table 2). One jay (Stuka) switched strategy entirely when a competitor  
343 was present - significantly selected the immediate over the delayed reward.

344

345 **Table 2. Delayed choices per individual across conditions for test trials only (high-quality reward in**  
 346 **delayed position).** Binomial exact two-tailed test:  $p < 0.05$  highlighted in bold. NC crows = New  
 347 Caledonian crow; E jays = Eurasian jay. In one case, Stuka made a majority of immediate choices  
 348 highlighted in italics as significant immediate, low-quality reward choice.

ID	Species	Choice	Alone (out of 16)	Competitor (out of 16)	Non-competitor (out of 16)	% Overall
Birute	NC crows	Delayed	16	16	16	100
		p-value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	
Fossey	NC crows	Delayed	16	16	16	100
		p-value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	
Irene	NC crows	Delayed	16	16	16	100
		p-value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	
Konrad	NC crows	Delayed	16	16	16	100
		p-value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	
Leakey	NC crows	Delayed	16	16	16	100
		p-value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	
Marie	NC crows	Delayed	15	15	16	95.83
		p-value	<b>0.0005</b>	<b>0.0005</b>	<b>&lt;0.0001</b>	
Godot	E jays	Delayed	13	7	12	68.75
		p-value	<b>0.0213</b>	0.804	0.0768	

Homer	E jays	Delayed	15	5	12	68.75
		p-value	<b>0.0005</b>	0.210	0.0768	
Penny	E jays	Delayed	13	9	9	64.58
		p-value	<b>0.0213</b>	0.804	0.804	
Sojka	E jays	Delayed	14	5	11	62.5
		p-value	<b>0.0042</b>	0.210	0.2101	
Stuka	E jays	Delayed	13	2	10	52.08
		p-value	<b>0.0213</b>	<b>0.004</b>	0.455	

349

## 350 Discussion

351

352 We tested the flexibility of the ability to employ delayed gratification, i.e. to wait for a delayed, higher-  
353 quality reward over an immediate, lower-quality one, in different social conditions in two corvid species  
354 that differ in sociality and food-caching, New Caledonian crows and Eurasian jays, using the rotating-tray  
355 paradigm. We found species and condition differences on choices to select an immediate, but lower-quality  
356 reward over a delayed, higher-quality one. Specifically, jays were more likely to select the immediate, low-  
357 quality reward than crows. Jays, though not crows, were also more likely to alter their choices while alone  
358 compared with when a competitor or a non-competitor was present. Crows continued to forgo the  
359 immediate, lower-quality reward for the delayed, higher-quality one irrespective of condition. Our findings  
360 highlight that the ability to delay gratification in Eurasian jays is influenced by the presence of conspecifics,  
361 depending on their identity (competitor/ non-competitor), suggesting flexibility in their delayed  
362 gratification abilities. On the other hand, the crows continue to delay gratification even with a competitor  
363 present, reflecting stability (or inflexibility) in their delayed gratification abilities. Furthermore, both



364 species were capable of delaying gratification in this paradigm, comparable with young children and other  
365 New Caledonian crows in a previous study [55] (S5 Resource), as well as capuchin monkeys (*Cebus Apella*)  
366 [56].

367 The species difference was unexpected, with the crows selecting the delayed, high-quality reward  
368 regardless of social condition, while the jays altered their choices when competitors or non-competitors  
369 were present. Both species were able to reliably delay gratification while alone, which was expected, given  
370 New Caledonian crows delayed gratification using the rotating tray paradigm in a previous study [55]. We  
371 note the jays took longer to train than the crows (crows: 2 sessions; jays 3-8 sessions to pass criterion) and  
372 three other jays did not pass criterion to proceed to testing (despite having 15-34 sessions of 10-trials per  
373 session). It is possible that species differences were a result of limitations of the study set-up or subject  
374 sourcing. Although both species were originally sourced in the wild, the jays had been hand-reared and  
375 housed long-term in captivity, whereas the crows were parent-reared and only temporarily held in captivity  
376 (~4 months). Both species received adequate habituation and were required to pass comparable criterion  
377 prior to testing. The jays were all adults, while the crows ranged in age (juvenile to adult). While there were  
378 no differences in choices between individual crows (Table 2), we do not have sufficient variation in the jay  
379 performance to test for age effects.

380 The type of competitor/ non-competitor was as comparable as possible between species. All subjects  
381 were familiar with their observing, non-focal conspecifics (NC crows caught together so potentially a  
382 family unit) although the prior interactions of the NC crows were unknown (being wild caught) (S1 Table).  
383 However, in the jays, the non-focal/ observer bird (competitor/ non-competitor) was not always the same  
384 individual across all trials, partly due to practical issues of encouraging the focal and non-focal to participate  
385 in each trial and partly due to more fluid dominance relationships. With the jays, it appeared that the  
386 dominance relationships varied between some pairs across the 6-month period of this study, hence, we  
387 conducted repeated food monopolization trials and assigned the non-focal accordingly (S1 & S2 Table).  
388 We also note that many of the jay breeding pairs in this captive colony change year-by-year. For both  
389 species, the food monopolization trials supported the distinction of a competitor versus non-competitor

390 status for the non-focal bird in relation to the focal bird. The food monopolization trials for the crows were  
391 limited to the group and conducted prior to testing due to field season time pressures. The crow test  
392 compartments were around twice the size of the jay compartments, so it is possible that the crow non-focal  
393 took longer to reach the platform, thereby potentially less likely to directly compete for rewards. The focal  
394 and non-focal (both species) were released simultaneously though to remedy this issue. Furthermore, we  
395 incorporated the requirement for the focal to lift a small lid to obtain the reward, once chosen, which created  
396 a short time delay between selection and eating/hiding the reward in their bill.

397 The species differed from one another in adult sociality (NC crows: family groups; E jays: territorial  
398 pairs) and food caching (NC crows: moderate; E jays: specialised cachers) [24, 53]. We selected adult  
399 sociality as it is more consistent than at the juvenile/ subadult stages and our sample consists primarily of  
400 adults. These socio-ecological factors could impact choices relating to food selection and responses to  
401 competition. We interpret these findings as a caching specialist with territorial pair living (E jays) showing  
402 flexibility or perhaps struggling to delay gratification when there is social competition, while a moderate  
403 caching and family-group living species (NC crows) continues to delay gratification - suggesting stability  
404 (or inflexibility) in behaviour regardless of social context. This flexibility by the E jays may relate to this  
405 change in behaviour being a more adaptive response to take any reward available immediately (even if less  
406 preferred), rather than risk waiting and end up without any reward at all, as the competitor may take it.

407 With regard to caching, the jays - being specialised cachers - have evolved under the social context of  
408 cache pilfering and development of cache protection strategies [46]. With sociality, the jays may be less  
409 tolerant of potential competitors, being more likely to actively displace conspecifics and defend territories,  
410 than the crows. Although not a highly social corvid species, the New Caledonian crows may form temporary  
411 aggregations of small groups [62] and will tolerate conspecifics outside of their family groups - largely  
412 juveniles and sub-adults (2-years old) - with rarely observed aggressive interactions [63]. Juvenile crows  
413 have been observed showing submissive displays when in the presence of non-family adults [63]. It is  
414 possible that stable hierarchies exist with the crows [63], similar to carrion crows (*Corvus corone*) [64].  
415 This is less likely with the Eurasian jays, given the variation observed in the food monopolization trials and

416 continuous changing of breeding pairs suggesting non-linear hierarchies (S2 Table), as well as the generally  
417 dyadic and territorial nature of Eurasian jays in the wild [24]. Species differences in responses to novel food  
418 and objects (i.e. neophobia) may influence performance [53], however, this is unlikely due to habituation  
419 and both species demonstrating a reliable ability to delay gratification in the alone condition (Table 2).

420 The condition effect in the Eurasian jays was largely in line with our expectations. The jays flexibly  
421 altered their choices depending on the social context, being more likely to take the immediate reward, even  
422 though of lower quality, rather than risk losing it to a competitor. They were more strongly influenced by a  
423 competitor than a non-competitor on the group-level. However, on the individual level, all five jays did not  
424 show significant differences between competitor and non-competitor trials as they still chose the immediate,  
425 low-quality reward in some trials in both conditions (Table 2). These findings may relate to a higher risk of  
426 being displaced and losing the reward to any conspecific.

427 These captive jays were hand-reared socially and live most of the time (outside of breeding season,  
428 when they live in pairs to reduce risk of aggression) in a large social group. This social setting is quite  
429 different to their natural behaviour in the wild, where when adult, they will largely defend territories in  
430 pairs [24]. Furthermore, in captivity, they are provided with adequate food for all individuals, distributed  
431 through-out the large aviary to reduce any competition. Whether or not jays living in the wild would also  
432 show this flexibility in behaviour in response to social context requires future focus. Regardless of these  
433 aspects of the captive setting, the jays appear to pay attention and respond to the presence and identity of  
434 others while delaying gratification, while the crows do not adjust their choices according to social  
435 competition. These findings are in line with previous studies on Eurasian jays testing flexibility of other  
436 behaviours in social contexts. For example, they are able to switch caching and pilfering behaviour  
437 depending on whether they are more subordinate or dominant than a conspecific present [46]. In addition,  
438 evidence suggests that Eurasian jays are also capable of desire state attribution towards both their partners  
439 and competitors [36, 65, 66] (although see [47]).

440 Future research can expand on species comparisons to explore social influences on self-control and  
441 other aspects of decision-making. For instance, using the rotating tray paradigm or other delayed

442 gratification paradigms in non-human primates and human children, or in highly social/tolerant species  
443 compared with less social/ tolerant ones within taxa. Expanding on the length of delay, as this study utilised  
444 only a short delay (15 seconds), the quantity (as we only tested using quality differences) and visibility of  
445 rewards provides several avenues for future work. Furthermore, it would be worthwhile to expand on the  
446 identity of the observer, for instance, to see whether familiarity or age influences choices in delayed  
447 gratification tests, in particular, whether NC crow delayed gratification is influenced by presence of other  
448 types of observers.

449

## 450 **Conclusion**

451 In conclusion, we explored social influences on delayed gratification in two corvid species - New  
452 Caledonian crows and Eurasian jays - highlighting both species and condition (alone, competitor, non-  
453 competitor) differences in performance. Both species were able to delay gratification. The jays did so  
454 flexibly depending on the social context, while the crows remained stable in their choices for delayed  
455 rewards. These findings contribute to our understanding of self-control and the factors influencing delayed  
456 gratification.

457

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462

## 463 **Additional Information**

464 The authors declare no competing interests.

465

## 466 **Author Contributions**

467 R.M. conceived and designed the experiments. Data collection was conducted by: 1) crow testing: M.S.  
468 and E.G-P. with supervision by R.M, A.H.T. and N.S.C; and 2) jay testing: J.D. and E.G-P. with supervision  
469 by R.M and lab direction from N.S.C. R.M. and J.D. planned the analysis and interpreted the data. R.M and  
470 J.D. analysed the data and prepared the figures and tables. R.M. and J.D. wrote the first draft of the  
471 manuscript, with subsequent drafts being reviewed by the other authors. R.M, A.H.T., R.D.G. and N.S.C  
472 provided direct funding support and coordinated the wider NC crows field season (A.H.T, R.D.G) and E  
473 jays Comparative Cognition lab (N.S.C, R.M). All authors gave final approval for publication and agreed  
474 to be accountable for all aspects of the work.

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483

## 484 **Ethics Statement**

485 The study methods were conducted in accordance with relevant guidelines and regulations. The Eurasian  
486 jay study was reviewed and approved by the University of Cambridge Animal Welfare Ethical Review  
487 Body (AWERB) and was conducted under a non-regulated license (NR2022/82). The New Caledonian  
488 crow research was conducted under approval from the University of Auckland Animal Ethics Committee  
489 (reference number 001823) and from the Province Sud with permission to work on Grande Terre, New  
490 Caledonia, and to capture and release crows.

491

## 492 **Data availability**

493 The full data set and R script is available on Figshare: 10.6084/m9.figshare.23514828 (private link:  
494 <https://figshare.com/s/3a6adfae2cb31f707659>)

495

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647

## 648 **Supporting Information Captions**

649

650 **S1 Table: Subject Information.** \*Change in relative dominance between sessions (see S2 Table).

651

652 **S2 Table: Food monopolization results for the Eurasian jays.** \*Change in relative dominance between  
653 two specific individuals.

654

655 **S3 Table. ‘Learning speed’ per individual and species: number of trials and sessions to reach**  
656 **criterion and complete test trials (last 2 sessions counted) in alone condition.** Three of eight jays did  
657 not reach criterion within 15 sessions (\*) so were excluded from further testing. NC crows = New  
658 Caledonian crows; E jays = Eurasian jays.

659

660 **S4 Resource. Example video trials for both species**

661

662 **S5 Resource. Comparison of baseline to Miller et al. 2020 [55]**

663

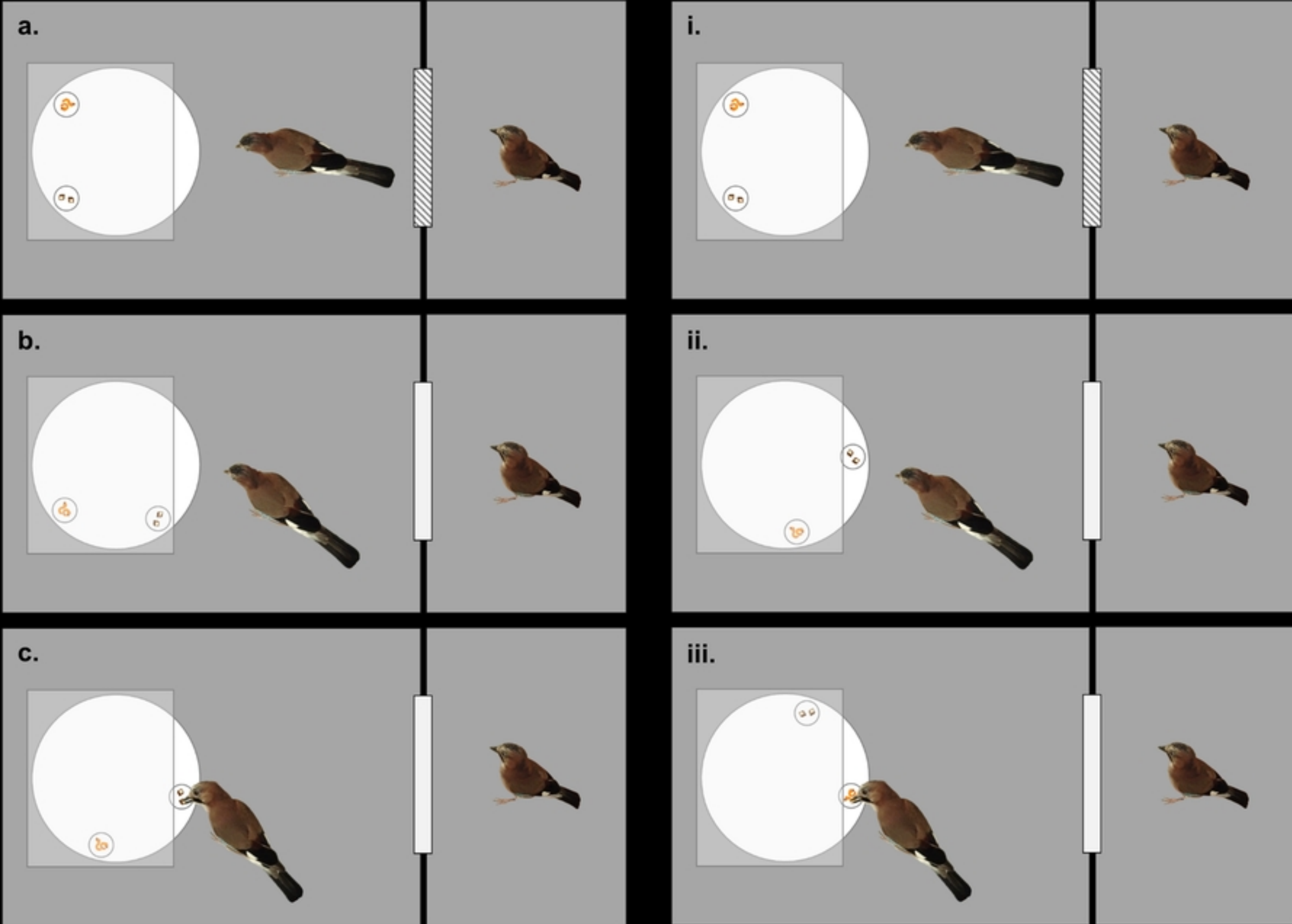


Fig.1

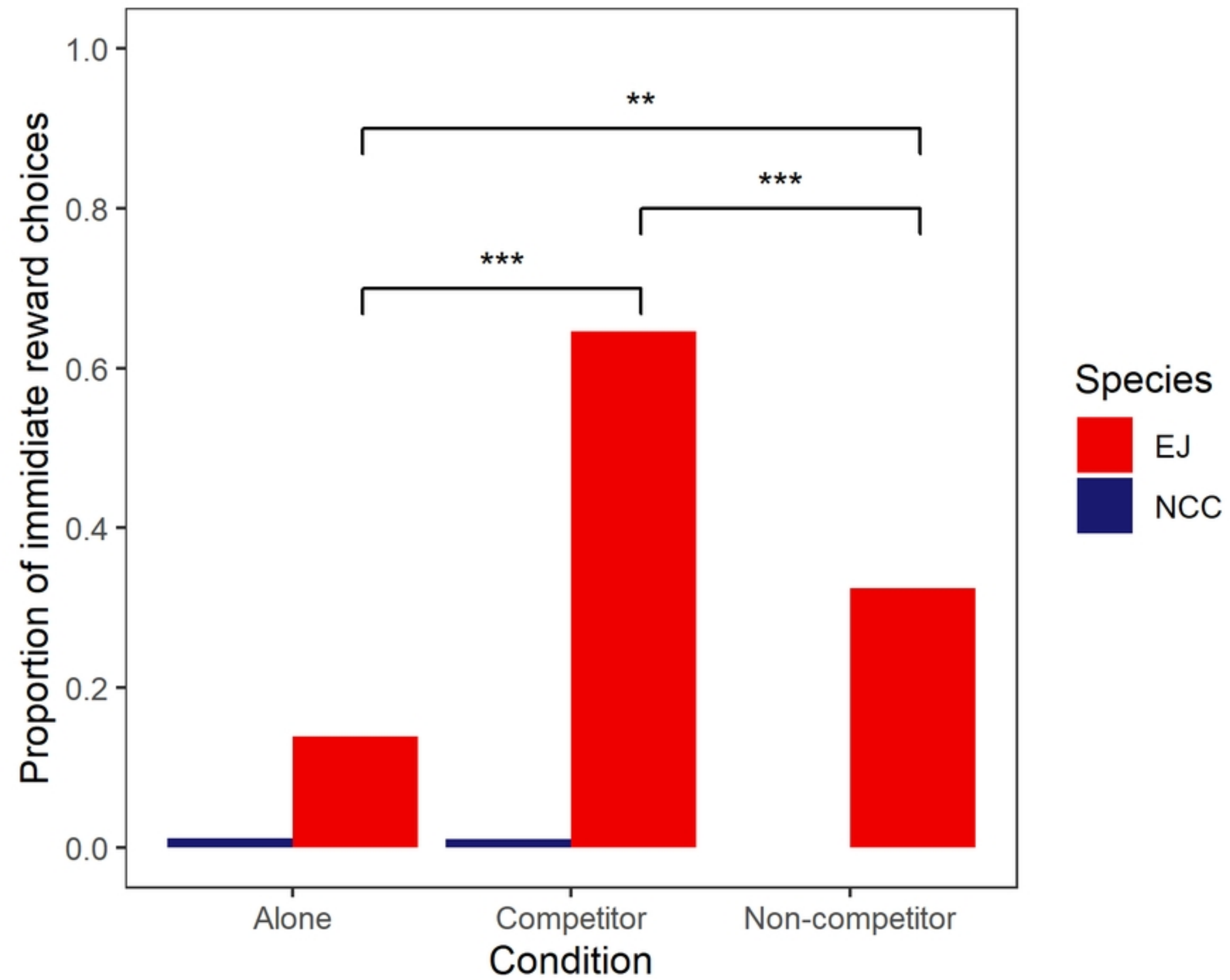


Fig.2