

1 **Individual repeatability, species differences, and the influence of socio-**  
2 **ecological factors on neophobia in 10 corvid species**

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38 Short title: The socio-ecological drivers of neophobia in corvids

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## 42 **Summary**

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44 Behavioural responses to novelty, including fear and subsequent avoidance of novel stimuli,  
45 behaviours referred to as neophobia, determine how animals interact with their environment.  
46 Neophobia aids in navigating risk and impacts on adaptability and survival. There is variation within  
47 and between individuals and species, however, lack of large-scale, comparative studies critically  
48 limits investigation of the socio-ecological drivers of neophobia. In this study, we tested responses to  
49 novel objects and food (alongside familiar food) versus a baseline (familiar food alone) in 10 corvid  
50 species (241 subjects) across 10 labs worldwide. There were species differences in the latency to  
51 touch familiar food in the novel object and food conditions relative to the baseline. Three of seven  
52 socio-ecological factors influenced object neophobia: 1) use of urban habitat (vs not), 2) territorial  
53 pair vs family group sociality and 3) large vs small flock size (whereas range, caching, hunting live  
54 animals, and genus did not); while only flock size influenced food neophobia. We found that, overall,  
55 individuals were temporally and contextually repeatable (i.e. consistent) in their novelty responses in  
56 all conditions, indicating neophobia is a stable behavioural trait. With this study, we have established  
57 a network of corvid researchers, demonstrating potential for further collaboration to explore the  
58 evolution of cognition in corvids and other bird species. These novel findings enable us, for the first  
59 time in corvids, to identify the socio-ecological correlates of neophobia and grant insight into specific  
60 elements that drive higher neophobic responses in this avian family group.

61

## 62 **Introduction**

63

64 Novelty is a common and vital aspect of animal life. The discovery of novel items and environments  
65 offers individuals an opportunity to benefit from new resources, such as food, tools, and shelter<sup>1,2</sup>.  
66 Animals navigate novel stimuli through exploration, which allows for the assessment of any potential  
67 utility. However, novelty also presents the potential for danger: unknown food may be toxic, unknown  
68 objects may be traps and unfamiliar species may be predators<sup>1</sup>. Consequently, various species also

69 show fear and subsequent avoidance of novel stimuli, behaviours referred to as neophobia. Neophobia  
70 acts as a protective behaviour, encouraging hesitance and vigilance before/during exploration and thus  
71 helping to limit the danger associated with novelty<sup>1</sup>. An appropriate level of neophobia within a  
72 species, according to their niche, should maximise their opportunity whilst minimising risk. As  
73 neophobia affects how animals interact with novelty, and novelty is a common occurrence, an  
74 understanding of neophobia is vital for animal cognition and behaviour research. This is particularly  
75 relevant as the world becomes heavily urbanised, with many species having to adapt to human-  
76 generated environmental changes and the inevitable novelty that follows<sup>3</sup>. An understanding of the  
77 mechanisms underlying neophobia and any influencing factors may help explain why some species  
78 are more successful in adapting to new environments than others.

79 Previous research has investigated factors that may influence neophobia, as levels of neophobic  
80 behaviour vary between species and even individuals within a species (e.g. parrots<sup>4</sup> and ungulates<sup>5</sup>).  
81 Many of these factors relate to socio-ecological factors, which may affect the costs and benefits of  
82 exploration and neophobia. However, there are very few large-scale comparative studies of  
83 neophobia, though one notable exception is Mettke-Hofmann et al. (2002) study on the relationship  
84 between a series of ecological factors, including diet and habitat, and both neophobia (latency to eat  
85 familiar food in presence of novel object) and exploration (latency to touch a novel object) behaviour  
86 in 61 species of parrot<sup>4</sup>. The results suggested that a species' ecology is closely associated with  
87 neophobia and exploration. Several different ecological variables influenced exploration, with species  
88 that inhabit complex habitats, have a diet of flower buds or fruits, and live on islands showing the  
89 shortest latencies in exploration tests. Two factors influenced neophobia: a diet of insects and a diet of  
90 leaves, indicating that parrots with a diet of insects were more neophobic than those feeding on plant  
91 material, explained as a possible consequence of the toxicity danger associated with insects<sup>4</sup>. Thus,  
92 increased neophobia may mediate some of this risk. We note that this study did not test for individual  
93 repeatability over time or between conditions, used primarily small sample sizes (range 1-23  
94 individuals, mean = 4.4, median = 2.5), and largely tested in uncontrolled social settings (e.g.  
95 measuring first individual to approach with/without others present)<sup>4</sup>.

96 Many smaller-scale studies have investigated individual ecological factors that may affect  
97 neophobia within species. For example, individual common myna birds (*Acridotheres tristis*) who  
98 inhabit urban environments demonstrate lower levels of neophobia than those from rural areas and are  
99 quicker to utilise novel food resources <sup>6</sup>. Greggor et al. (2016) found that wild birds (five corvid  
100 species, seven other bird species) approached human litter objects faster in an urban environment than  
101 in a rural environment <sup>7</sup>. These findings have been suggested to occur because of habituation: birds in  
102 urban areas encounter human litter and objects more frequently than those in rural areas and thus  
103 become accustomed to this particular type of novelty. Other explanations have focussed on how urban  
104 areas offer low-risk and high-benefit environments, with a vast array of food resources in the form of  
105 human litter, and low levels of predation <sup>8</sup>.

106 Differing habitats and diets may also influence neophobia and exploration. Greenberg and Mettke-  
107 Hofmann (2001) hypothesised that the costs of neophobia outweigh the benefits for generalist species,  
108 who utilise a range of resources that vary in availability, so reduced neophobia would allow for  
109 frequent exploration and discovery of new resources <sup>1</sup>. However, specialist species, who use fewer,  
110 more stable resources, should show greater levels of neophobia as they have limited need to explore  
111 new food sources. This has been supported by research indicating that generalist Lesser-Antillean  
112 Bullfinch (*Loxigalla noctis*) showed shorter latencies to approach novel feeding stations than  
113 specialist bananaquit (*Coereba flaveola*) <sup>9</sup>. Similarly, generalist song sparrows (*Melospiza melodia*)  
114 were less neophobic of objects than specialist swamp sparrows (*Melospiza georgiana*) in the field and  
115 in the lab <sup>10,11</sup>.

116 Furthermore, social context, such as the presence of conspecifics, has been shown to reduce  
117 neophobia and increase exploration in several species. For example, zebra finches (*Taeniopygia*  
118 *guttata*) showed shorter latencies to eat from a novel feeder when in a flock than when alone <sup>12</sup>. This  
119 may be due to group presence reducing generalised fear and/or risk being shared, thus reducing  
120 neophobia <sup>12</sup>. It may also be context specific. For instance, Stöwe et al. (2006) found that ravens  
121 (*Corvus corax*) approached novel objects faster in the presence of siblings than non-siblings <sup>13</sup>.  
122 Ravens who are classed as “slow” explorers showed reduced latencies to approach novel objects when  
123 with a “fast” conspecific than when alone, but fast individuals’ approaches were impeded by

124 conspecifics<sup>13</sup>. Further, Chiarati et al. (2012) found that dominant breeding males in kin-based groups  
125 of carrion crows approached novel food before their other family members, reducing risks for their  
126 partner and offspring<sup>14</sup>.

127 Individual differences in neophobia and exploration have been shown to be stable traits (i.e.  
128 repeatable or consistent over time and contexts) in some species, though inconsistent in others, which  
129 may be influenced by a range of factors, including the species, task, measures used, as well as  
130 seasonality, developmental, and social influences<sup>4,14-16</sup>. Furthermore, although several socio-  
131 ecological variables appear to influence neophobia, a lack of large-scale comparative research limits  
132 interpretation of these effects (with the notable exception of<sup>4</sup>), as well as testing whether it is a stable  
133 behavioural trait<sup>17</sup>. Consistent methodology within a multi-species study allows for effective  
134 comparison within and between species<sup>18</sup>, and thus would contribute towards understanding the  
135 mechanisms and influences of neophobia.

136 As a behavioural trait that dictates much of an animal's interaction with the environment, including  
137 how they approach and solve novel problems, such data are valuable not only for establishing links  
138 between behaviour and ecology but also for studying cognition. Indeed, the time taken to learn a  
139 foraging task in feral pigeons (*Columba livia*) and zenaida doves (*Zenaida aurita*) covaried with  
140 individual levels of neophobia<sup>19,20</sup>. Variation in neophobia also presents a potential confound for  
141 cognition research, as it can impact on performance in comparative cognitive tests, though is most  
142 often not tested or accounted for in relation to such comparisons between species<sup>20</sup>. Outside of basic  
143 research, neophobia data may help inform applied animal welfare and conservation, including pre-  
144 release training in reintroduction programmes<sup>21</sup>. For instance, working to increase neophobia levels  
145 in animals subjected to culling due to conflict with farmers<sup>21</sup>.

146 Corvids (members of the crow family) are often featured in cognitive research<sup>22</sup>, and are known to  
147 be relatively high on the scale of neophobia<sup>2,23</sup>. Within corvids, species and individuals differ in  
148 neophobic propensities<sup>7,24-26</sup>, as well as socio-ecological factors, such as range (how geographically  
149 widespread a species is), sociality, caching (hiding food for later use) behaviour, and tool-use<sup>22,27-31</sup>.  
150 It is currently unknown what drives neophobia in corvids, for instance, whether they follow the same  
151 pattern as parrots relating to diet type e.g.<sup>4</sup>, or whether there are different drivers of this variation.

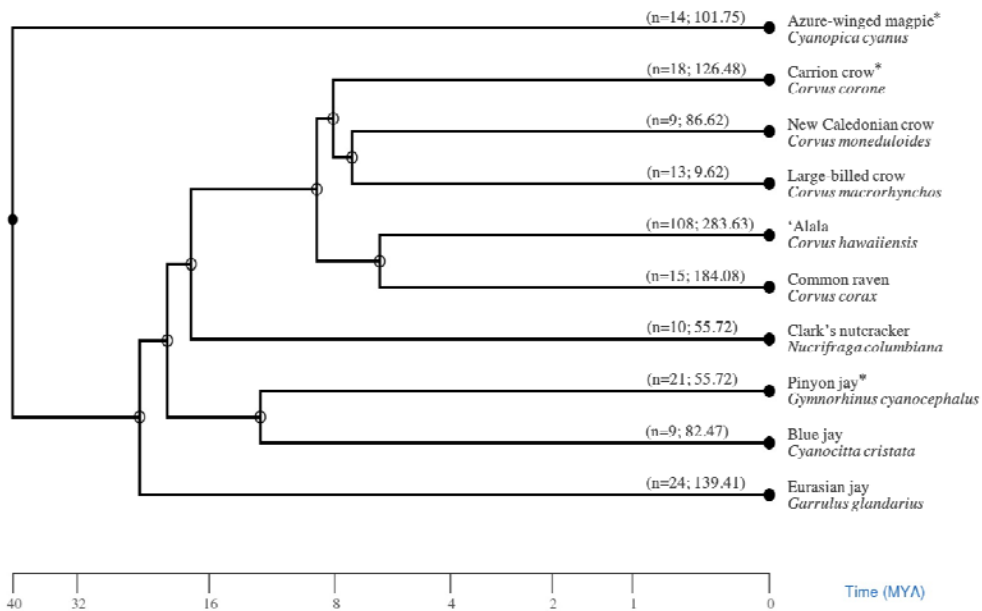
152 Corvids are therefore an optimal choice for these questions, however, to our knowledge, no study has  
153 yet compared neophobia comprehensively across many different corvid species, with repeated testing  
154 for individual repeatability, and directly testing the influence of socio-ecological factors.

155 We conducted a multi-lab collaborative study with three main aims: 1. compare neophobia across  
156 species 2. investigate the effect of socio-ecological factors on neophobia, and 3. assess individual  
157 temporal and contextual repeatability in neophobia. In 10 corvid species (241 subjects: Figure 1), we  
158 tested behavioural responses - specifically latency to touch familiar food – in three conditions: novel  
159 objects, novel food, and control condition (familiar food alone), with each condition repeated 3 times  
160 over 6-8 weeks (3 test rounds, 1 trial per condition per round, repeated every ~2 weeks). Individuals  
161 were primarily tested while alone to control for any social influences and allow for repeated  
162 individual testing. Novel items were presented with familiar food to ensure behavioural responses  
163 were a result of the conflict between neophobia and desire for the familiar food, rather than, for  
164 example, exploration<sup>1</sup>. Our response variable tested true food (and object) neophobia (i.e. fear of the  
165 appearance of the food), rather than dietary conservatism (i.e. latency to consume a novel food  
166 regularly in the diet)<sup>32</sup>. We pooled resources across labs with the aim of increasing sample sizes and  
167 species representation. We selected tests that were not too time or labour intensive, given many labs  
168 were invited to contribute data, whilst giving a meaningful comparison across species that is largely  
169 based on established methodologies (i.e. latency to eat/ approach familiar food in the presence of a  
170 novel item).

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172 **Figure 1. Phylogenetic tree.** Sourced from <http://www.timetree.org> with sample size (n=x) and  
173 relative object neophobia score per species (mean latency to touch familiar food difference score i.e.  
174 novel object minus control value) - higher score indicates higher neophobic response to novel object.

175 \* donates species tested at 2 sites



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Firstly, we compared food and object neophobia between corvid species. We expected to find some species differences, as indicated by previous comparative corvid research e.g. <sup>7,25</sup>. Next, we tested for the influence of socio-ecological factors: range (broad vs restricted/endemic), use of urban habitats (in addition to suburban/rural), hunting live animals, adult sociality (territorial vs family groups), flock size (small vs large), food caching (moderate vs specialised), and genus (*Corvus* or not) on neophobia. We expected that, like diet in parrots <sup>4</sup>, neophobia would relate closely to aspects of species ecology. Specifically, in line with some previous research, we expected that species inhabiting a broad range, and utilising urban habitats, would show lower neophobia compared to those in restricted ranges and using only sub-urban/rural areas <sup>6-9,11,33</sup>. Lower neophobia was also expected from species that live in larger flocks and family groups compared to small flocks and territorial pairs, due to the potential of risk-sharing between larger groups <sup>12,34</sup>. As the influence of live hunting (selected as the species tested were otherwise generalists), caching and genus have not been previously tested in similar species, we had no a priori predictions for these factors. Finally, we tested for individual temporal and contextual repeatability. We expected to find individual repeatability, as there were only short delays between test rounds (~2 weeks), similar to a related study in 'A (*Corvus hawaiiensis*)<sup>34</sup>.



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## 194 **Results**

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### 196 **1. Species differences**

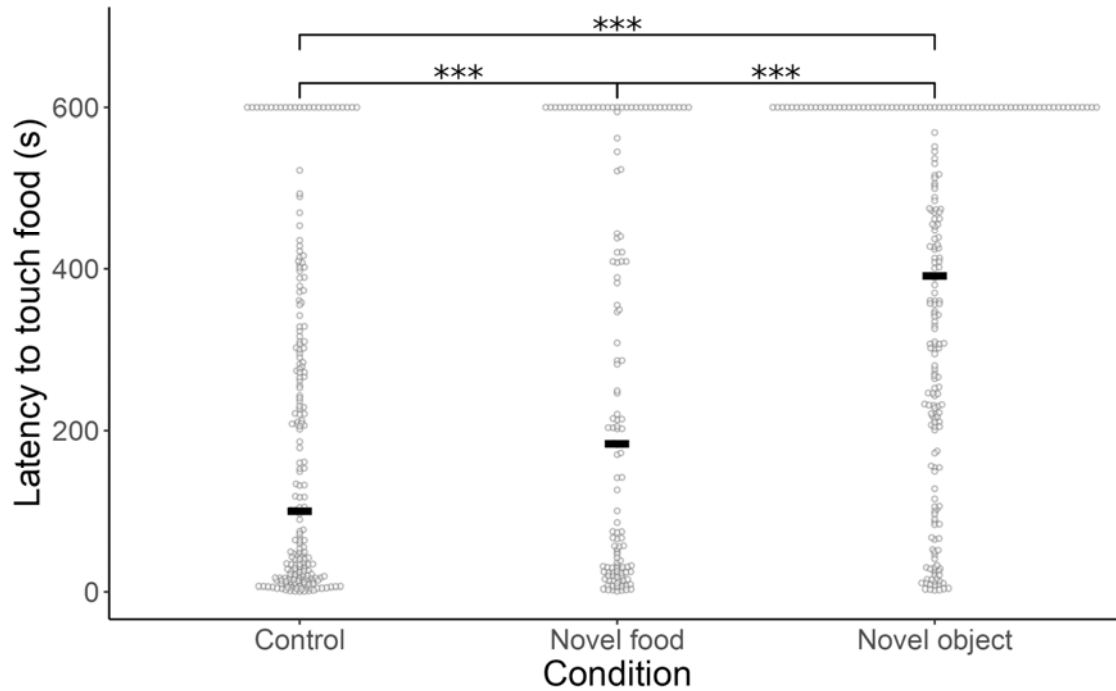
197

198 Latency to touch familiar food differed across conditions (LMM:  $X^2=316.05$ ,  $df=2$ ,  $p<0.001$ ), test  
199 rounds ( $X^2=28.75$ ,  $df=1$ ,  $p<0.001$ ), and species ( $X^2=93.03$ ,  $df=9$ ,  $p<0.001$ ). The birds waited longer  
200 with a novel object or novel food present compared to the control condition (Tukey contrasts: novel  
201 object – control,  $z=18.79$ ,  $p<0.001$ ; novel food – control,  $z=7.97$ ,  $p<0.001$ ), and they waited longer  
202 when a novel object was present than when a novel food was present ( $z=7.35$ ,  $p<0.001$ ) (Figure 2).  
203 While latency to touch familiar food did not differ between rounds 1 and 2 (Tukey contrasts:  $z=0.57$ ,  
204  $p=0.371$ ), it decreased in round 3 compared with round 1 and 2 (rounds 1 – 3,  $z=4.94$ ,  $p<0.001$ ;  
205 rounds 2 – 3,  $z=4.35$ ,  $p<0.001$ ) (S1 Figure). We also found that latency differed across species (S1  
206 Table; Figure 3).

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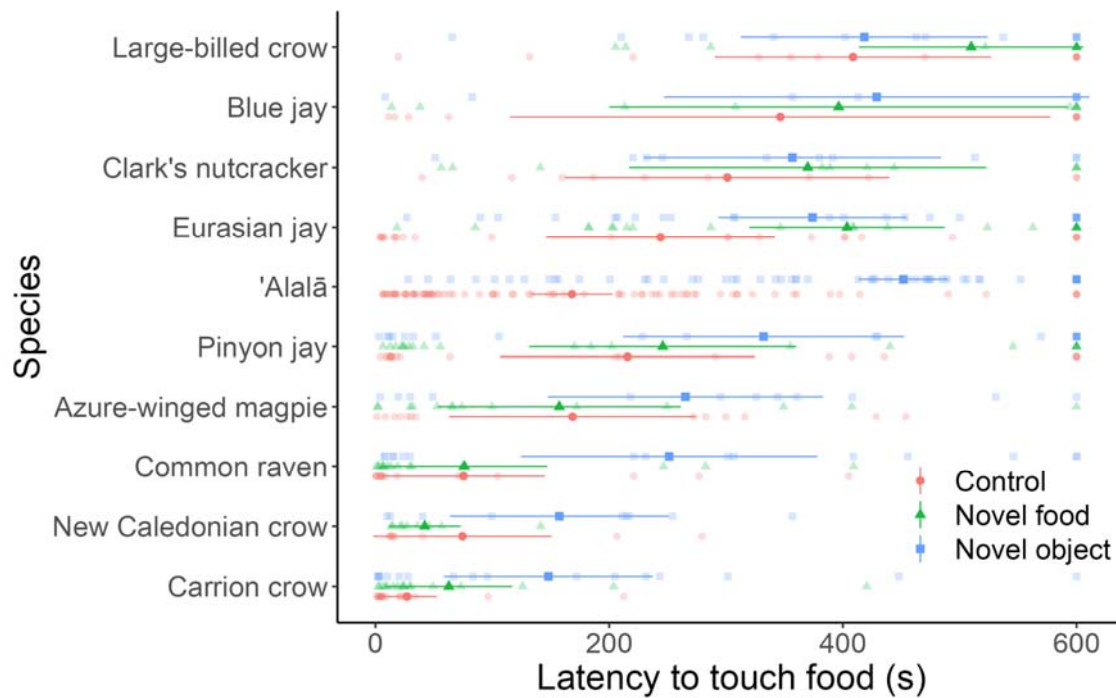
#### 208 **Figure 2. Latency to touch familiar food in each condition across all species**

209 Control, novel food, and novel object conditions all differed from each other. Points represent  
210 individuals, lines represent median. \*\*\*  $p < 0.001$



211

212 **Figure 3. Latency to touch familiar food in each condition for each species.** Some species differed  
 213 in mean latency. Individual points represent subject means over rounds, points with error bars  
 214 represent species means and 95% confidence intervals.



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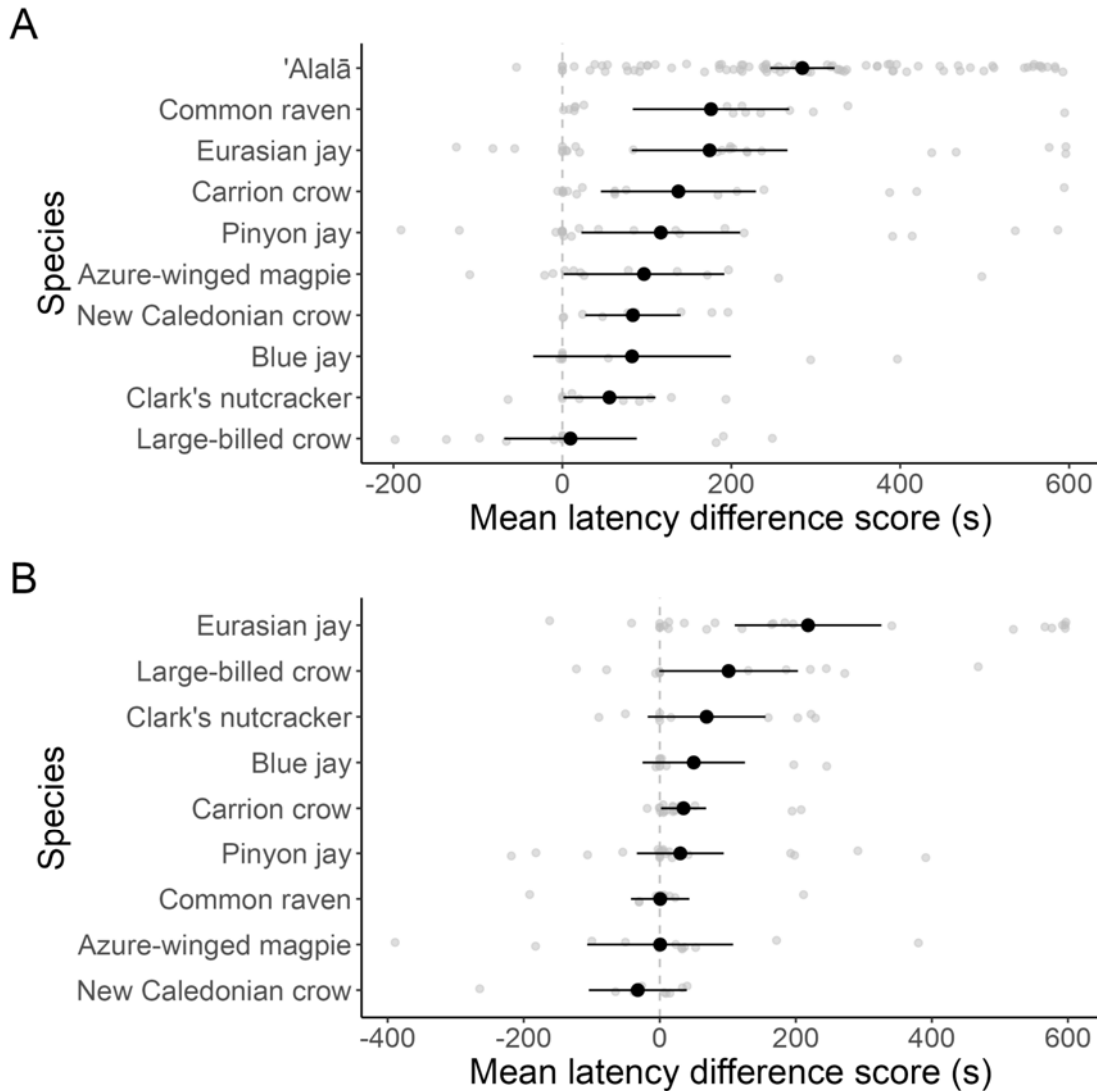
216 However, a potential confound of this study is that most species were housed and tested at different  
217 sites and therefore site is largely correlated with species. Three species were tested at two different  
218 sites. Using exploratory analysis, within these three species, we found that site did not affect latency  
219 to touch familiar food in carrion crows or azure-winged magpies but did affect latency in pinyon jays  
220 (S2 Table; S2 Figure).

221 To aid in standardizing latencies across sites as well as control for baseline neophobia and current  
222 motivational state, we created pairwise difference scores by subtracting the control latencies from the  
223 novel object and novel food latencies for each round and individual. Positive difference scores  
224 represent slower approaches to familiar food when a novel object/food is present (neophobia) and  
225 negative difference scores represent faster approaches (neophilia). The novel object difference scores  
226 differed across species (LMM:  $X^2=47.02$ ,  $df=9$ ,  $p<0.001$ ) and round ( $X^2=8.18$ ,  $df=1$ ,  $p=0.017$ ), with  
227 some differences between pairs of species (S3 Table; Figure 4A). Using novel object difference  
228 scores, common ravens were more neophobic than azure-winged magpies, large-billed crows, New  
229 Caledonian crows, Clark's nutcrackers, blue jays and pinyon jays; azure-winged magpies, pinyon jays  
230 and Eurasian jays were more neophobic than large-billed crows; Eurasian jays were more neophobic  
231 than blue jays and Clark's nutcrackers; carrion crows were more neophobic than Clark's nutcrackers  
232 and large-billed crows; 'Alala' were more neophobic than blue jays, large-billed crows, Clark's  
233 nutcrackers, New Caledonian crows, pinyon jays (Figure 4A).

234

235 **Figure 4. Species comparison using difference scores.** Mean latency difference scores varied across  
236 species for (A) novel object neophobia and (B) novel food neophobia. Positive difference scores  
237 represent slower approaches to familiar food when a novel item was present (i.e. neophobia) and  
238 negative difference scores represent faster approaches (i.e. neophilia). Points represent individuals.

239



240

241 The novel food difference scores also differed across species ( $\chi^2=23.49$ ,  $df=8$ ,  $p=0.003$ ) but not round

242 ( $\chi^2=5.58$ ,  $df=2$ ,  $p=0.062$ ). Note that 'A' species were not tested in the novel food condition and are

243 removed from this analysis. Using novel food differences scores, Eurasian jays were more neophobic

244 than all other species (Figure 4B; S4 Table). Overall, for both object and food conditions, most

245 species were neophobic with mean difference scores greater than 0, with only New Caledonian crows

246 showing a negative mean difference score for the food condition.

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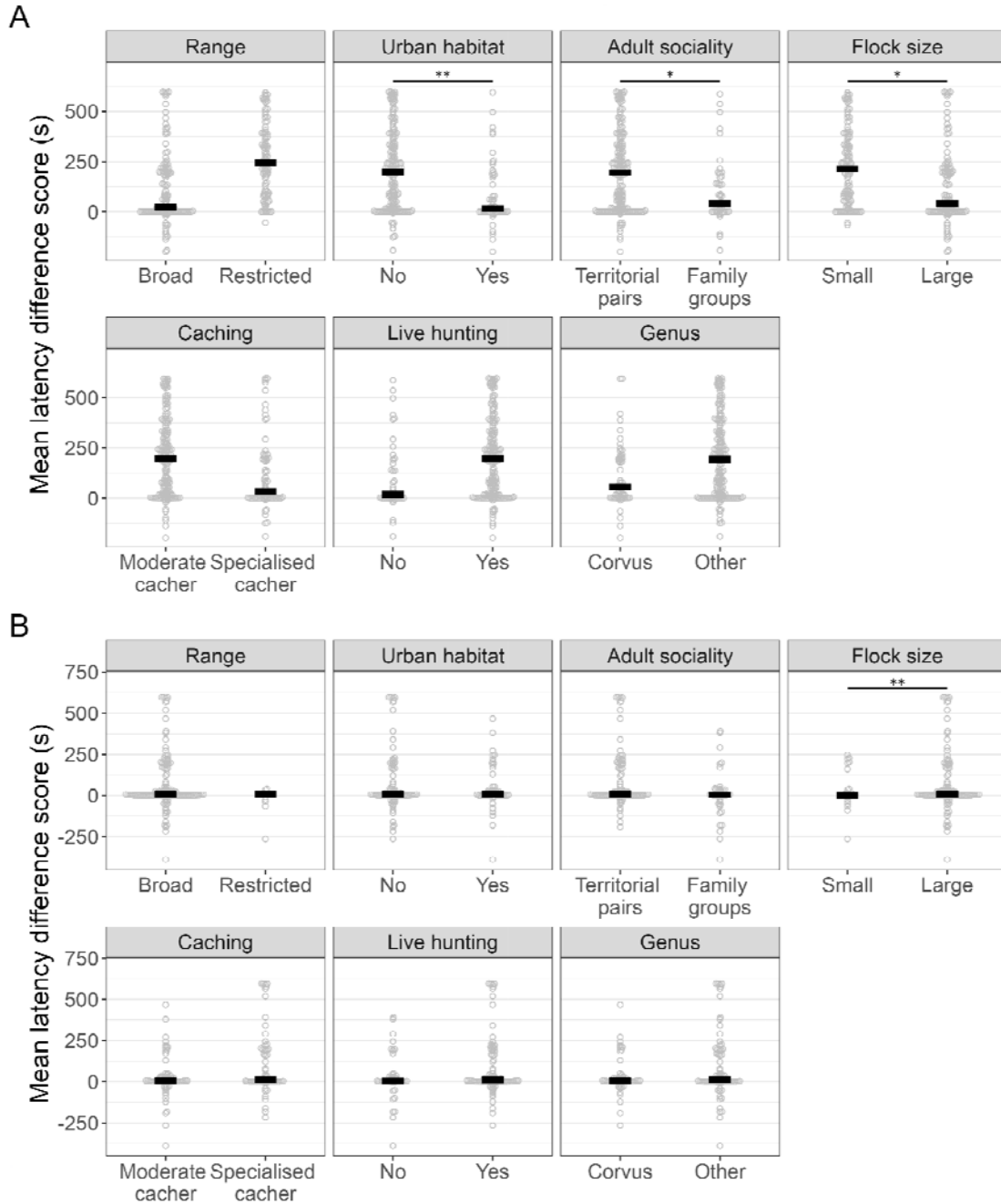
248 **2. Effect of socio-ecological factors**

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250 Using novel object difference scores, object neophobic responses were affected by urban habitat use  
251 ( $X^2=7.23$ ,  $df=1$ ,  $p=0.007$ ), adult sociality ( $X^2=6.61$ ,  $df=1$ ,  $p=0.010$ ), and flock size ( $X^2=4.98$ ,  $df=1$ ,  
252  $p=0.026$ ), but not range ( $X^2=0.59$ ,  $df=1$ ,  $p=0.443$ ), caching ( $X^2=2.78$ ,  $df=1$ ,  $p=0.100$ ), live hunting  
253 ( $X^2=2.36$ ,  $df=1$ ,  $p=0.125$ ), or genus ( $X^2=0.24$ ,  $df=1$ ,  $p=0.628$ ). Specifically, species that use urban  
254 habitats (as well as other habitats), live in larger flocks and family groups were less neophobic than  
255 those that do not/ very limited use of urban habitats, live primarily in territorial pairs or in smaller  
256 flocks (Figure 5A). Using novel food difference scores, food neophobia was only affected by flock  
257 size ( $X^2=8.99$ ,  $df=1$ ,  $p=0.003$ ) and not range ( $X^2=2.72$ ,  $df=1$ ,  $p=0.100$ ), urban habitat ( $X^2=0.33$ ,  $df=1$ ,  
258  $p=0.564$ ), adult sociality ( $X^2=1.98$ ,  $df=1$ ,  $p=0.160$ ), caching ( $X^2=0.25$ ,  $df=1$ ,  $p=0.621$ ), live hunting  
259 ( $X^2=0.10$ ,  $df=1$ ,  $p=0.756$ ), or genus ( $X^2=3.55$ ,  $df=1$ ,  $p=0.060$ ). In contrast to the object neophobia  
260 finding, species that typically live in small flocks were less neophobic of novel food than those living  
261 in large flocks (Figure 5B).

262

263 **Figure 5. Effect of socio-ecological factors on neophobia.** Linear mixed model on socio-ecological  
264 factors affecting latency to touch familiar food, using difference scores showed effects of urban  
265 habitat, adult sociality, and flock size on novel object neophobia (A) and effect of flock size on novel  
266 food neophobia (B). Positive difference scores represent slower approaches to familiar food when a  
267 novel object is present (i.e. neophobia) and negative difference scores represent faster approaches (i.e.  
268 neophilia). Points represent individual subjects and horizontal bars represent medians.



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270

### 271 **3. Individual temporal and contextual repeatability**

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273 Across all species, individuals' responses to novel stimuli were temporally repeatable across test

274 rounds (1-3) and contextually repeatable across conditions (control, novel object, novel food) (intra-

275 class correlation coefficient:  $N = 217$ ,  $ICC = 0.462$ ,  $p < 0.001$ ,  $CI = 0.402-0.521$ ). In addition, responses  
276 were temporally repeatable within each condition (control:  $N = 216$ ,  $ICC = 0.542$ ,  $p < 0.001$ ,  $CI =$   
277  $0.467-0.625$ ; novel object:  $N = 215$ ,  $ICC = 0.548$ ,  $p < 0.001$ ,  $CI = 0.469-0.625$ ; novel food:  $N = 132$ ,  
278  $ICC = 0.477$ ,  $p < 0.001$ ,  $CI = 0.381-0.591$ ) (S5 Table). A within-species analysis showed similar  
279 temporal repeatability except for the New Caledonian crows (all conditions), azure-winged magpies  
280 (novel food only) and large-billed crows (novel object only), with contextual repeatability in all  
281 species except for the New Caledonian crows (S5 Table, S6 Table). Note that ‘Alala’ were not tested  
282 in the novel food condition.

283

## 284 **Discussion**

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286 In our multi-lab collaborative study, we tested the responses (latency to touch familiar food) of 10  
287 corvid species to novel objects and food (beside familiar food), compared with a control baseline  
288 condition (familiar food alone). We found: a) some species differences in latency to touch familiar  
289 food in the presence of a novel object or novel food relative to baseline, b) effects of three socio-  
290 ecological factors - urban habitat use, adult sociality, and flock size - on object neophobia, and an  
291 effect of flock size on food neophobia, and c) individual temporal and contextual repeatability across  
292 species, as well as within species for all species except New Caledonian crows (all conditions), azure-  
293 winged magpie (novel food) and large-billed crow (novel object). The novel object and novel food  
294 conditions elicited higher neophobic responses (i.e. higher latencies) than the control condition.  
295 Additionally, neophobic responses reduced across rounds, with lower latencies in round 3 of testing  
296 than either round 1 or 2.

297 Species differed in object and food neophobia. For instance, we found that: common ravens,  
298 ‘Alala’ and Eurasian jays were more neophobic than most other species tested for object neophobia,  
299 with Eurasian jays being more neophobic than all other species for food neophobia (using difference  
300 scores). The mean difference scores showed primarily neophobic responses to novel items (i.e.  
301 positive scores) compared to neophilic responses (i.e. negative scores). The critical test for

302 interpreting these species differences, which is not possible in most of the previous research with  
303 single or small numbers of species/ individuals, was to test for specific influences of several socio-  
304 ecological factors that naturally differ between these corvid species. We found that three of seven  
305 factors tested influenced object neophobia: urban habitat use, adult sociality and flock size, while  
306 range, caching, hunting live animals and genus did not. Specifically, object neophobia was lower in  
307 species using urban habitats (n=5 species), living in family groups (n=3) and large flocks (n=6)  
308 compared with those only using suburban/ rural areas (n=5 species), living primarily in territorial  
309 pairs (n=7), or small flocks (n=4). Only flock size influenced food neophobia, with those living in  
310 small flocks showing lower neophobia than those in large flocks.

311 We expected urban habitat use to influence neophobia, based on previous research in other species,  
312 such as within-species comparisons in common myna <sup>6</sup> and black-capped chickadees <sup>33</sup>. Urban  
313 habitats typically provide environments that are rich in novel stimuli, including human litter and  
314 manmade structures. Consequently, individuals and species inhabiting these areas are frequently  
315 exposed to various types of novel objects and may become habituated to such novelty. The costs of  
316 neophobia may also outweigh the benefits in urban habitats: human objects may become useful  
317 resources (litter may contain food or be an effective tool), an opportunity that would be lost by a high  
318 neophobic response. Additionally, urban environments have a relatively low predation risk for corvids  
319 and other animals, thus limiting the dangers associated with exploration of novel objects <sup>8,12</sup>.

320 Similarly, we expected sociality to influence neophobia, with lower object neophobia in large  
321 flocks or family groups due to increased risk-sharing, compared with species living primarily as  
322 territorial pairs while adult or small flocks <sup>12</sup>. Social presence has been shown in some species,  
323 including corvids, to have either a facilitating or inhibiting effect on neophobia and exploration <sup>15,27,35</sup>.  
324 We differentiated species as ‘territorial’ vs ‘family groups’ according to their most prevalent social  
325 organisation <sup>28</sup>. Some of these species do have quite flexible systems based on fission-fusion, such as  
326 common raven <sup>36</sup>, thereby, they may be territorial as adults and/or during breeding season but be fairly  
327 tolerant of one another as juveniles or outside of breeding season <sup>37</sup>. We therefore included a second  
328 sociality related factor: ‘small’ (up to 100 individuals) vs. ‘large’ flocks (over 100 individuals). It is



329 interesting to note that we see contrasting effects of flock size on object compared with food  
330 neophobia, and effects of sociality even with individual testing (i.e. tested while alone).

331 We did not find an effect of hunting live animals on food or object neophobia (hunting live  
332 animals n=6 species vs not n = 4), which was our main dietary related measure, as otherwise, these  
333 corvids are largely similar in their diets. We may see a stronger effect of this factor with different  
334 types of novel food or in predator neophobia tasks. There was no effect of caching, despite differences  
335 between moderate (n=6 species) and specialised cachers (n=4) in the amount and type of food items  
336 that they cache. Our caching differentiation was based on a categorization of food caching into low,  
337 moderate, and specialized species<sup>38</sup> (Table 1), though it should be noted that some corvids also cache  
338 objects<sup>38,39</sup>. However, there was insufficient prior data available to differentiate all species according  
339 to variation in the amount and type of object caching. Should this data become available in future, it  
340 would be worth testing our data to explore whether object cachers also differ in neophobia.

341 We found no effect of range (broad n=8 vs restricted n=2 species) on either food or object  
342 neophobia, which was unexpected, according to the “island tameness theory”, which suggests that  
343 island populations may be less neophobic because they have evolved with fewer dangers in the  
344 environment<sup>40</sup>. We note, however, that only the New Caledonian crows and ‘Alala’ had a restricted  
345 i.e. endemic range, therefore interpretation of this finding should be tentative, particularly as the New  
346 Caledonian crows were wild sourced. Finally, we found no effect of genus (Corvus n=5 or not n=5  
347 species) on neophobia. Should additional reliable phylogenetic data for corvids become available, and  
348 we were able to increase the number of species above 20 species<sup>16,41,42</sup>, we should be able to include  
349 further phylogenetic controls in future.

350 All species, other than New Caledonian crows (all conditions), azure-winged magpies (novel food)  
351 and large-billed crows (novel object) showed individual repeatability over time (i.e. between 3 rounds  
352 over ~6-8 week period). Similarly, all species, except for New Caledonian crows, showed individual  
353 repeatability across all 3 conditions. Regarding the lack of individual repeatability in New Caledonian  
354 crows, these were the only wild birds (temporarily captive) of the sample, which may have influenced  
355 their responses. It is also possible that this is related to habituation to the captive situation. Individual  
356 flexibility (i.e. lack of repeatability or inconsistency) may be more adaptive in the wild, where

357 conditions can vary more widely than captivity. Additionally, individual inconsistency has been found  
358 in other corvid species, including pinyon jays and Clark's nutcrackers exploratory responses to novel  
359 environments and novel objects (without familiar food present)<sup>16</sup>. Some of these same individuals  
360 were tested in the present study, highlighting that neophobia may vary within and between individuals  
361 depending on types of neophobia, or aspects of study design, like task type.

362 The main limitations of this study, also applicable to some previous comparative cognition studies,  
363 were some unavoidable site differences. We therefore primarily used difference scores (novel  
364 condition minus control data) to aid in standardising latency scores across sites and control for  
365 baseline neophobia. We differentiated each of the socio-ecological factors tested on 2-levels, relying  
366 on published data to support these distinctions (e.g.<sup>27,38</sup>), as it was not otherwise possible to determine  
367 each species reliably by other means. Some factors could be explored on further levels (such as a scale  
368 or distribution size for range) if supporting evidence becomes available for each species for such a  
369 distinction in future. There were differences in sample size per species, indicating care should be  
370 taken with any generalisations beyond the samples to wider species-levels. Our samples were also  
371 primarily captive individuals, which may influence neophobia<sup>43</sup>. This study was a worthwhile and  
372 necessary first step into establishing a multi-lab collaboration, and captive birds allowed us to identify  
373 individuals, conduct repeated testing and control the environment, which could be expanded upon in  
374 future, for instance, to include corvids in the field<sup>7</sup>. Being able to test more widely within groups of  
375 the same species from different backgrounds, as well as between species, and expanding these types  
376 of collaborative approaches to test other bird groups than corvids to explore the drivers of neophobia  
377 in birds more generally, is a recommended focus on future research. Furthermore, other aspects of  
378 neophobia, such as novel environments, predators or humans (e.g.<sup>25</sup>) could be tested.

379 There are several wider implications of our study. When comparing neophobia in different species,  
380 it is important, where possible, to consider the role of socio-ecological factors, like diet, habitat use  
381 and sociality. Neophobia can influence how an animal interacts with novel problems, so should be  
382 tested as a baseline, particularly in new species/individuals, when conducting cognition research. The  
383 world is fast becoming more urbanised due to human activity, with many species being forced to  
384 adapt to changing environments or risk survival<sup>3</sup>. As neophobia may impact how quickly a species or

385 individual can adapt, it is a useful tool in designing conservation applications, such as in  
386 reintroductions<sup>21,34,44</sup>. For example, the presentation of new bird feeders or safe nesting sites could be  
387 modified according to the species individual's level of neophobia, and more neophobic individuals  
388 may require more pre-release training than others. Additionally, for species which are extinct in the  
389 wild, comparative behavioural and cognitive data from close relatives may help determine the extent  
390 to which long-term conservation breeding erodes natural responses. Therefore, neophobia and related  
391 research can provide valuable information in basic and applied research.

392 In conclusion, this study established a global collaborative network among corvid researchers to  
393 investigate the socio-ecological correlates of neophobia in these birds. Furthermore, neophobia can  
394 impact cognitive performance<sup>19,44</sup>, but is often not tested or accounted for in comparative research –  
395 this study contributes to resolving this issue. It also contributes to a growing push to conduct multi-  
396 species comparisons while simultaneously facilitating other collaborative work between these labs in  
397 the future. Though species differences in neophobia are well-known among those working with  
398 corvids, they are more typically incorporated into study designs (for example, including a habituation  
399 phase to new stimuli) than studied in their own right or comparatively across different species. By  
400 investigating neophobia across species that vary in several socio-ecological factors and feature  
401 frequently in studies of behaviour and cognition, this study has broad implications for those interested  
402 in behavioural ecology, evolutionary biology, comparative psychology and other related fields.

403

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419

#### 420 **Author contributions**

421 R.M., M.L.L., A.F. A.L.G., N.S.C. conceived the study idea and research design. R.M. and M.L.L.  
422 project managed the study. R.M., S.A.R. and J.R.S. analysed the data, R.M., M.L.L. and J.R.S  
423 produced the figures. R.M., A.F., K.F.B., E.G.P., K.G., L.B.L., A.L.G., Y.L., M.S., A.K., P.S., L.W.,  
424 L.M.W., Y.Z. collected the data. R.M., A.F., I.C., E.G.P., A.L.G. coded the videos. R.M. and I.C.  
425 wrote the manuscript, with comments and feedback from all other authors. R.M., K.B., T.B., K.G.,  
426 E.I., D.M.K., Z.L., A.N., J.R.S., A.H.T., N.S.C. provided funding to support the study.

427

#### 428 **Declaration of interests**

429 The authors declare no competing interests.

430

#### 431 **Main-text Figure/ Table Legends**

432 **Figure 1. Phylogenetic tree.** Sourced from <http://www.timetree.org> with sample size (n=x) and  
433 relative object neophobia score per species (mean latency to touch familiar food difference score i.e.  
434 novel object minus control value) - higher score indicates higher neophobic response to novel object.

435 \* donates species tested at 2 sites

436

#### 437 **Figure 2. Latency to touch familiar food in each condition across all species**

438 Control, novel food, and novel object conditions all differed from each other. Points represent  
439 individuals, lines represent median. \*\*\* p < 0.001

440

441 **Figure 3. Latency to touch familiar food in each condition for each species.** Some species differed  
442 in mean latency. Individual points represent subject means over rounds, points with error bars  
443 represent species means and 95% confidence intervals.

444

445 **Figure 4. Species comparison using difference scores.** Mean latency difference scores varied across  
446 species for (A) novel object neophobia and (B) novel food neophobia. Positive difference scores  
447 represent slower approaches to familiar food when a novel item is present (i.e. neophobia) and  
448 negative difference scores represent faster approaches (i.e. neophilia). Points represent individuals.

449

450 **Figure 5. Effect of socio-ecological factors on neophobia.** Linear mixed model on socio-ecological  
451 factors affecting latency to touch familiar food, using difference scores showed effects of urban  
452 habitat, adult sociality, and flock size on novel object neophobia (A) and effect of flock size on novel  
453 food neophobia (B). Positive difference scores represent slower approaches to familiar food when a  
454 novel object is present (i.e. neophobia) and negative difference scores represent faster approaches (i.e.  
455 neophilia). Points represent individual subjects and horizontal bars represent medians.

456

457 **Table 1. Socio-ecological factors of corvid species tested**

458

## 459 **STAR Methods**

460

### 461 **Subjects**

462 We tested 241 corvid subjects (141 males, 95 females, 5 unknown, primarily adult birds) across 10  
463 species and 10 lab teams worldwide (S8 Table). The sample sizes ranged from 9 to 108 subjects per  
464 species (mean = 24; median = 15), depending on subject availability. All subjects could be identified  
465 individually (e.g. by coloured leg rings). Species tested were common ravens (n=15), carrion/ hooded  
466 crows (n=18), large-billed crows (n=13), New Caledonian crows (n=9), ‘Alala’ (n=108), Eurasian  
467 jays (n=24), pinyon jays (n=21), blue jays (n=9), Clark’s nutcrackers (n=10) and azure-winged

468 magpies (n=14). Each lab housed their own species according to the ethical and housing conditions  
 469 required within each country, with two labs holding more than 1 species, and 3 species each tested at  
 470 two different sites (S8 Table). Individual labs were responsible for the data collection of their birds  
 471 but were provided with the same protocols to ensure the methodology remained consistent and were  
 472 in regular contact with the organising team.

473 These species differ in several specific socio-ecological factors (Table 1). Information was collated  
 474 as to whether species occupied a broad or restricted range (e.g. island-living endemic species), use of  
 475 urban habitats (as well as rural and suburban), whether they hunt live birds and mammals, live in  
 476 territorial pairs (primarily throughout the year or seasonally) or within family groups (e.g. dominant  
 477 breeding pair with offspring), average flock size (small = up to 100 individuals, large = over 100  
 478 individuals), whether they cache (hide food to return to later) large amounts of a specific food during  
 479 certain seasons (specialised) or a variety of food across the year (moderate), and if they were from the  
 480 *Corvus* genus or not <sup>27,38,45-47</sup>.

481

482 **Table 1. Socio-ecological factors of corvid species tested**

Species	Range	Urban habitat	Hunting live animals	Food caching	Adult sociality	Flock size
Common raven, <i>Corvus corax</i>	Broad	*No	Yes	Moderate	Territorial pairs	Large
Carrion/ hooded crow, <i>Corvus corone</i> ; <i>C. cornix</i>	Broad	Yes	Yes	Moderate	** Territorial pairs	Large

Large-billed crow, <i>Corvus macrorhynchos</i>	Broad	Yes	Yes	Moderate	Territorial pairs	Large
New Caledonian crow, <i>Corvus moneduloides</i>	Restricted	No	No	Moderate	Family groups	Small
Alala, <i>Corvus hawaiiensis</i>	Restricted	No	Yes	Moderate	Territorial pairs	Small
Eurasian jay, <i>Garrulus glandarius</i>	Broad	Yes	Yes	Specialised	Territorial pairs	Large
Pinyon jay, <i>Gymnorhinus cyanocephalus</i>	Broad	No	No	Specialised	Family groups	Large
Blue jay, <i>Cyanocitta cristata</i>	Broad	Yes	No	Specialised	Territorial pairs	Small
Clark's nutcracker, <i>Nucifraga columbiana</i>	Broad	No	Yes	Specialised	Territorial pairs	Small

Azure-winged magpie, <i>Cyanopica cyanus</i>	Broad	Yes	No	Moderate	Family groups	Large
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483 Differentiation within factors restricted to 2 levels reflecting availability of published data to support  
484 these distinctions across all species. \* Typically applicable for Europe (where the common ravens  
485 tested in this study were held and sourced); ravens have used/use cities at some North American sites  
486 (personal communication, Thomas Bugnyar). \*\* One carrion crow population in Spain have helpers at  
487 the next (i.e. cooperative breeding), though this is not reported in other populations<sup>48</sup>  
488

## 489 **Apparatus/materials**

490 There were three conditions: control (familiar food alone), novel food, and novel object (novel items  
491 beside familiar food). The familiar food (placed in a familiar food bowl) varied between bird groups,  
492 depending on the regular diet in each lab. The novel food consisted of jelly in 3cm<sup>3</sup> blocks, also  
493 placed in a (different) familiar food bowl. There were three colours/flavours of jelly used: orange,  
494 purple/blackcurrant, and green/lemon & lime, which were presented individually across the three  
495 rounds. As the species typically have different diets, and the food needed to be equally novel for them  
496 all, a colourful, human-made food such as jelly provided an ideal option (with prior ethical approval  
497 including from a Home Office appointed Named Veterinary Surgeon, Cambridge University). The  
498 novel objects came in three variations, but all had the same properties: they were made of multiple  
499 items and textures, with no part that could look like eyes (to avoid resembling predators), and all  
500 contained the colours blue, yellow, green, and red<sup>34</sup>. Part of the objects also had to be shiny, and the  
501 objects were all between one third and one half the size of the subject (so the size of the object itself  
502 varied with species; S3 Figure). All birds were tested in a feeding or testing compartment/cage, which  
503 varied in dimensions by lab, but gave the birds as much room as possible to avoid and/or approach  
504 stimuli. The testing area was familiar to the bird, or else the bird was habituated to the cage prior to  
505 testing.



506

## 507 **Procedure**

508       The tests involved measuring behavioural responses to novel food and novel objects beside  
509 familiar food, in relation to baseline measures of familiar food only (control). Data collection took  
510 place outside of breeding season, with adult, captive individuals, other than the New Caledonian  
511 crows, which were wild birds temporarily held in captivity. For most species/groups, individuals were  
512 temporarily separated in visually isolated testing compartments, though typically not acoustically  
513 isolated i.e. could hear groupmates ('Alala' were left in their regularly housed social groups for tests  
514 to reduce stress, which were primarily 2-bird breeding pairs). Separation was achieved via voluntary  
515 participation in some labs (e.g. Eurasian jays, New Caledonian crows, common ravens, 'Alala', as  
516 well as – in T.B. & J.J.M.M. lab - carrion crows and azure-winged magpies), while the other birds  
517 were physically moved by an experimenter to the familiar testing area as per the typical testing  
518 procedures in each lab. The novel item (food or object) was placed beside the familiar food dish  
519 (20cm for larger species i.e. *Corvus* genus, 10cm for smaller species i.e. other species), with items  
520 placed in the same location (e.g. a table/ platform/ mesh wall – large enough so that the bird could  
521 approach slowly from more than a body length away) for all tests and individuals within each species.  
522 Where possible, the stimuli were present before the subject entered the testing compartment (all  
523 species except ravens). The test trial started when the subject entered the testing compartment (or  
524 experimenter left compartment). Each trial lasted a maximum of 10 minutes (600 seconds) or ended  
525 when the subject touched the familiar food (i.e. beak contacted food).

526       Each novel test 'round' was conducted 3 times with 1 trial per condition per round (i.e. 9 trials in  
527 total) to allow for testing for individual repeatability within and between conditions. The control trial  
528 was conducted within 48 hours of both novel tests, and all in the morning, without withholding of  
529 food before testing if possible. Each round of testing (1 trial each of food- control-object conditions)  
530 took place with approx. 2 weeks between each round i.e. week 1: food-control-object, week 3: food-  
531 control-object, week 5: food-control-object. Therefore, testing took approximately 6 weeks in total to  
532 complete per species/group. The order of presentation of the novel food and objects was

533 counterbalanced across subjects, e.g. subject 1, round 1 – novel food type 1 (orange jelly), round 2 –  
534 type 2 (green jelly), round 3 – type 3 (purple jelly); subject 2, round 1 – type 3, round 2 – type 1,  
535 round 3 – type 2 etc. The testing schedule for half of the subjects was food-control-object in every  
536 round, and for the other half object-control-food in every round per group. All species were tested in  
537 all three conditions, except for the ‘Alala’s, which were tested in the familiar food and novel object  
538 conditions only<sup>34</sup> (due to Covid-19 pandemic limiting access for testing the novel food condition).  
539 Most individuals participated in all trials, with minimal missing data (S8 Table).

540 Our main measure was latency to touch familiar food signifying how long the individual took to  
541 touch a familiar, desirable food in the presence of a novel item. Any avoidance of the novel item (and  
542 thus familiar food) can then be interpreted as neophobia<sup>1</sup>. Latency to touch familiar food was used  
543 (rather than latency to eat) to control for any potential doubt as to whether the bird swallowed the  
544 food.

545

## 546 **Data Analyses**

547 Trials were recorded and all new videos (>1200 videos were newly collected; >650 ‘Alala’ videos  
548 were coded previously for<sup>34</sup> study) were coded in Solomon Coder. 12-15% of video trials for each  
549 species/group were coded by a second coder to ensure inter-rater reliability: ‘Alala’: intra-class  
550 correlation coefficient (ICC) = 0.956, CI = 0.94-0.97,  $p < 0.001$ ; all other species: ICC = 0.879,  
551 CI = 0.804-0.925,  $p < 0.001$ ). The full corresponding dataset for all analysis and the R script is  
552 available at: <https://figshare.com/s/16a77c3ab4e7569f0d98>

553 We had three main research questions and associated analyses: 1. species comparison 2. effect of  
554 socio-ecological factors 3. individual temporal and contextual repeatability of neophobia. The main  
555 dependent variable was latency to touch familiar food (0-600 seconds). We used R (version 4.1.0) for  
556 all analysis. For Q1: we conducted a Linear Mixed Model (LMM) to assess which factors influenced  
557 latency to touch familiar food. The residuals of a LMM visually approached normal distribution  
558 (although the Shapiro-Wilk test indicated the distribution was different from normal,  $W=0.9919$ ,  
559  $p < 0.001$ ). We compared the LMM (packages `lm4`, `car`, functions `lmer()`, `anova()`, and `Anova()`) with

560 the raw latency scores with an LMM using a log (base 10) transformation of latency + 1 (to avoid 0s).  
561 A likelihood ratio test (using `anova()` function) showed that the log-transformed model was preferred  
562 over the raw latencies (AIC raw = 21934.6, AIC log10 = 2761.5). Further transformations and  
563 Generalized Linear Mixed Models with other error distributions and link functions did not improve  
564 model fit. We therefore used the log-transformed latencies for all analysis, though we plot the raw  
565 latencies for visual clarity. With all LMMs, we used likelihood ratio tests to investigate the effect of  
566 the individual predictors (using `drop1()` function with best-fit model as input and setting test statistic  
567 to chi-square). We used Tukey comparisons (package `multcomp`, function `glht()`) for post-hoc tests  
568 without direct p-value correction. P-value corrections, such as Bonferroni, limit the number of  
569 possible comparisons<sup>49</sup> and comparison of multiple species was a primary aim in this study.

570 In LMM 1, using all data, we included the main effects of condition, species, and round in the  
571 full model, with individual nested in site as a random effect and all variables set as factors. A potential  
572 confound of our study is that most species were housed and tested in differing locations and  
573 conditions, including testing compartment size. Site is therefore correlated closely with species.  
574 However, three species were tested at two locations; therefore, we checked these three species  
575 individually for an effect of site (LMM, site as main effects, individual as random effect; S2 Table).

576 To directly examine potential neophobia effects of novel objects and food, we calculated  
577 difference scores by subtracting the log-transformed latency values of the control condition from  
578 those of the novel object condition and separately for the novel food condition. Therefore, the control  
579 serves as the baseline for how long it usually takes an individual to touch familiar food (without novel  
580 items present). By subtracting this control value from the latency to touch familiar food when a novel  
581 object was present should help to standardize for any site differences like cage size, e.g. species A has  
582 a small test cage so may have a shorter control latency due to this (less space to cover/ more likely to  
583 be closer at the start of the test) compared with species B with a large test cage. We created pairwise  
584 individual difference scores for each round and individual (e.g. individual 1, novel object round 1  
585 minus control round 1; novel object round 2 minus control round 2). In LMM 2 (object difference  
586 scores) and LMM 3 (food difference scores), we included the main effects of species and round, with  
587 individual nested in site as the random effect.

588 For Q2: we conducted LMM 4 (object difference score) and LMM 5 (food difference score), with  
589 the main effects of range, urban habitat, adult sociality, flock size, caching, live hunting, and genus,  
590 with individual nested in site as a random effect. The full models (including all predictor variables)  
591 had the best fit according to AIC. Though accounting for phylogenetic relationships can be important  
592 in some situations, testing for phylogenetic signal with fewer than 20 species is problematic<sup>41,42,50</sup>,  
593 testing is not advisable for all research questions (e.g. Q1)<sup>50</sup>, and the corvid evolutionary tree is not  
594 yet well established for all tested species (e.g. conflicting genetic results about the closest relative for  
595 ‘Alala□’<sup>51</sup>). Therefore, we did not include a phylogenetic control in our analyses. We did, however,  
596 include the variable ‘genus’ (Corvus or not) in our Q2 models. Additionally, we provide a  
597 phylogenetic tree for visualisation purposes with relative neophobia scores per species (Figure 1). In  
598 reporting all results, we avoid using the term ‘significant’<sup>52</sup>.

599 For Q3, we tested across species and within species for individual repeatability over time (across  
600 rounds) and over context (across conditions) using intraclass correlation coefficients (ICCs). We  
601 extracted ICC estimates from linear models with individual as a random effect and bootstrapped 1,000  
602 samples to generate 95% confidence intervals around the estimates (R package rpt, using rpt()  
603 function). For contextual repeatability, we included condition in the linear model, and for temporal  
604 repeatability, we included round in the model.

605 The ‘Alala□ control and novel object data was collected and examined in a previous study<sup>34</sup>. We  
606 used a comparable methodology as this study while collecting all the new data with the 9 new corvid  
607 species for the present study. We edited the ‘Alala□ data set for the present study by introducing a  
608 cut-off of maximum of 10 minutes for each trial (original data set maximum of 60 min trials) – any  
609 individuals that did not touch familiar food within 10 minutes were assigned 600 seconds – to ensure  
610 comparability.

611

612 Example video trials can be found at: <https://youtu.be/Lhzyk3srm dg>.

613

614 **Ethics Statement**

615 For animal research, all applicable international, national and/or institutional guidelines for the care  
616 and use of animals were followed. For N.S.C.'s Comparative Cognition lab, this non-invasive  
617 behavioural study with birds was conducted adhering to UK laws and regulations and was covered  
618 under a non-regulated procedure through University of Cambridge, approved by the Home Office  
619 appointed Named Animal Care and Welfare Officer, Named Veterinary Surgeon and Chairperson for  
620 the Psychology and Zoology Department Animal User's Management Committee. For D.M.K lab,  
621 research protocol approved by University of Manitoba's Animal User Committee (F18-041) and  
622 complied with the guidelines set by the Canadian Council on Animal Care. For A.N., experiments  
623 were approved by the national authorities (Regierungspräsidium). For E.I. lab, the experimental  
624 protocol (number 9069) authorised by the Animal Care and Use Committee of Keio University, for  
625 capturing wild crows (numbers 27924005 and 29030001) authorised by the Japanese Ministry of the  
626 Environment. For J.R.S. lab, research protocol approved by University of Nebraska-Lincoln IACUC  
627 (number 1708). For A.G. contribution, work was approved by San Diego Zoo Global's animal care  
628 and use committee IACUC (number 16-009) and conducted under USFWS Permit (number TE-  
629 060179-5) and State of Hawaii Division of Forestry and Wildlife permit (number WL16-04). For K.G.  
630 lab, a research protocol approved by Luther College IACUC (no. 2019-4). For A.H.T. lab, a  
631 University of Auckland Animal Ethics Committee (no. 001823). For T.B. lab, work on foraging  
632 decisions, including this non-invasive behavioural study, was conducted adhering to Austrian law (2.  
633 Federal Law Gazette no. 501/1989) and approved by an Animal Ethics and Experimentation Board of  
634 the Faculty of Life Sciences, University of Vienna. For Z.L. lab, the study was conducted according to  
635 the Ethics Review Committee of Nanjing University (no. 2009-116), under Chinese law, no specific  
636 approval was required for this non-invasive study.

637

## 638 **Supplemental Information Legends**

639

640 **S1 Figure. Latency to touch familiar food in each round, across all conditions and species.**

641 Round 3 differs significantly from round 1 and 2, while round 1 and 2 do not differ significantly from  
642 each other. Points represent individuals, lines represent median. \*  $p < 0.05$

643

644 **S2 Figure. Site effect on latency to touch familiar food in azure-winged magpie, carrion crow  
645 and pinyon jay**

646

647 **S3 Figure. Example of novel objects for Eurasian jays**

648

649 **S1 Table. Pairwise comparisons of latency data between species**

650

651 **S2 Table. Linear mixed models with main effect of site on latency to touch familiar food for the  
652 three species that were tested in two sites**

653

654 **S3 Table. Pairwise comparisons of novel object difference scores between species**

655

656 **S4 Table. Pairwise comparisons of novel food difference scores between species**

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658 **S5 Table. Individual temporal repeatability within each species and condition**

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660 **S6 Table. Individual contextual repeatability within each species**

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662 **S7 Table. Individual temporal and contextual repeatability**

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664 **S8 Table. Subject information, including sex, source and participation in testing**

665

666 **References**

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