

1 Testing relationship recognition in wild jackdaws (*Corvus monedula*)

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19 According to the social intelligence hypothesis, understanding the challenges faced by social
20 animals is key to understanding the evolution of cognition. In structured social groups,
21 recognising the relationships of others is often important for predicting the outcomes of
22 interactions. Third-party relationship recognition has been widely investigated in primates,
23 but studies of other species are limited. Furthermore, few studies test for third-party
24 relationship recognition in the wild, where cognitive abilities are deployed in response to
25 natural socio-ecological pressures. Here, we used playback experiments to investigate
26 whether wild jackdaws (*Corvus monedula*) track changes in their own relationships and the
27 relationships of others. Females were presented with 'infidelity simulations': playbacks of
28 their male partner copulating with a neighbouring female, and their male neighbour
29 copulating with another female, against a congruent control. Our results showed substantial
30 inter-individual variation in responses, but females did not respond more strongly to
31 infidelity playbacks, indicating that jackdaws may not attend and/or respond to relationship
32 information in this experimental context. Our results highlight the need for further study of
33 relationship recognition and other cognitive traits that facilitate group-living in the wild,
34 particularly in non-primates and in a wider range of social systems.

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41 Introduction

42 The social intelligence hypothesis posits that the sophisticated cognitive abilities seen in
43 some species may have arisen due to the selection pressures associated with group living^{1,2}.
44 Several studies provide support for the social intelligence hypothesis, linking cognitive
45 performance or brain size measures with various aspects of sociality²⁻⁷. However, other
46 studies have shown conflicting results⁸⁻¹⁰ (see ^{11,12} for a detailed discussion) and the social
47 intelligence hypothesis remains controversial. To determine whether social life favours the
48 evolution of associated cognitive abilities, it is necessary to understand how these cognitive
49 abilities help individuals to navigate a dynamically changing social world.

50 Social species must solve ecological challenges within a social context^{12,13}. In these cases,
51 the ability to recognise other group members and remember past interactions allows
52 individuals to predict (and potentially manipulate) others' behaviour¹⁴. Although obtaining,
53 processing and applying this knowledge is likely to be cognitively demanding^{5,13,15},
54 individuals who are more socially competent may derive fitness benefits as a result¹⁶⁻¹⁸. In
55 social groups where relationships persist over time, being able to track the relationships of
56 other group members can be useful in predicting the outcomes of interactions¹⁴. Knowledge
57 of third-party relationships might allow individuals to adjust their own behaviour
58 appropriately to avoid conflict¹⁹⁻²², solicit and provide support during agonistic
59 interactions^{5,23-27}, and take advantage of mating opportunities²⁸. Third-party relationship
60 recognition has been demonstrated in several primate species, originally leading some
61 authors to suggest that this ability may be confined to the primate order^{29,30}. Observations
62 of agonistic interactions indicate that bonnet macaques (*Macaca radiata*) solicit support
63 from individuals who are higher-ranking than their opponent²³ and chimpanzees (*Pan*

64 *troglydytes*) will modify their recruitment screams depending on the dominance rank of
65 bystanders²⁶. Playback experiments also provide evidence that primates track third-party
66 relationships. For instance, vervet monkeys *Chlorocebus aethiops pygerythrus*²⁰ and chacma
67 baboons *Papio hamadryas ursinus*¹⁹ respond to simulated reversals in the existing
68 dominance hierarchy, demonstrating an understanding of the dominance relationships
69 between other group members. Chimpanzees (*P. troglodytes*) will avoid aggressive
70 individuals who are socially bonded to their former opponent, for several hours following an
71 agonistic encounter²¹; and male baboons (*P. hamadryas ursinus*) track consortships between
72 other males and females in order to obtain sneaky matings²⁸. In vervet monkeys (*C.*
73 *aethiops*), playbacks of infant distress calls cause nearby females to look towards the
74 infant's mother, demonstrating recognition of mother-offspring relationships within the
75 social group³¹.

76 Few studies have investigated third-party relationship recognition in non-primates, despite
77 many other species living in complex societies where this ability is expected to be useful. For
78 example, hyenas (*Crocuta crocuta*) live in complex social groups with multiple hierarchically
79 structured matriline, similar to many primate societies¹⁴. Hyenas will join conflicts to
80 support the higher-ranking individual even if the subordinate member of the fighting dyad is
81 more aggressive, implying knowledge of the dominance relationships that exist in the
82 group²⁴ (but see ³²). Not only is it important to examine a diverse range of species, but also a
83 diversity of social systems – for instance, little is known about the value of third-party
84 relationship recognition in monogamous systems. Among birds, monogamy is the most
85 common social system and has been argued to be central to the evolution of avian
86 cognition⁵, although little is known about the cognitive demands associated with
87 maintaining long-term pair bonds. Furthermore, many monogamous bird species live in

88 groups and form stable, individualised relationships with others in addition to their breeding
89 partner⁵. Corvids exhibit this type of social system, and their sophisticated cognitive abilities
90 make them ideal subjects for investigating the evolution of social cognition³³⁻³⁵. Many
91 corvids form long-term pair bonds and live in colonies characterised by strict dominance
92 hierarchies between bonded pairs³⁶. Empirical evidence supports the idea that recognising
93 social relationships is beneficial in corvid colonies^{35,37}. For example, playback experiments
94 show that captive ravens (*Corvus corax*) respond to dominance rank reversals, both within
95 their own social group and in a neighbouring group²². Furthermore, observations of wild
96 ravens indicate that victims will reduce the frequency of their distress calls during agonistic
97 encounters, if the bonding partner of their aggressor is present in the vicinity; victims also
98 call more frequently when their own kin are nearby²⁷. Anecdotal reports suggest that rooks
99 (*Corvus frugilegus*) engage in redirected aggression, where individuals are more likely to
100 attack their aggressor's partner, or the aggressor of their partner, after a fight⁵. Finally,
101 ravens will intervene in the affiliative interactions of others that appear to be establishing a
102 strong bond, which is likely to require knowledge of the relationships of group members³⁸.

103 In the only experimental test of third-party relationship recognition in corvids to date,
104 Massen et al.²² found that ravens (*C. corax*) become stressed and engage in more self-
105 directed behaviour after hearing simulated encounters that violate their expectation of the
106 existing dominance hierarchy within their own colony. Male subjects also exhibited
107 decreased calling and attention behaviour following simulated rank reversals in a
108 neighbouring group, suggesting that ravens deduce third-party relationships by observation
109 alone. However, this study was conducted under controlled conditions using captive
110 individuals, where subjects could observe interactions between conspecifics very frequently.
111 Consequently, it is not clear to what extent these results reflect the cognitive abilities

112 animals employ in the wild, where a greater number of stimuli compete for individual
113 attention^{15,39,40}. Furthermore, most of the research carried out under natural conditions has
114 involved observations of naturally-occurring behaviour, and there is a lack of experimental
115 evidence for third-party relationship recognition in the wild outside the primate order. To
116 this end, a recent study by Pardo et al.⁴¹ describes the first experimental field test for third-
117 party relationship recognition in a non-primate. This study found that acorn woodpeckers
118 initiate defensive behaviour more quickly in response to calls from two birds from different
119 social groups, compared to calls of two birds from the same social group, suggesting that
120 individuals recognise group membership outside of their own social group. However, it is
121 not clear to what extent this indicates knowledge of the dyadic relationship between the
122 two callers, or whether it is possible that subjects were responding to the unfamiliar
123 stimulus of two calls occurring together when those calls had only been heard separately in
124 the past. Consequently, much remains to be determined as to the extent of third-party
125 relationship recognition in non-primates in the wild.

126 To address this research gap, we conducted an experiment to test whether wild jackdaws (a
127 social corvid, *Corvus monedula*) track changes in their own relationships and the
128 relationships of other members of their social group. This ability is likely to be useful in
129 jackdaw society: pairs form monogamous bonds and females assume the rank of their male
130 partner in the breeding colony's strict linear dominance hierarchy⁴². These hierarchies
131 remain relatively stable over time due to high adult survivorship (c. 80%, although estimates
132 vary) and low rates of 'divorce'⁴³. For jackdaws, tracking relationships within the colony may
133 allow individuals to avoid conflict with more dominant pairs, especially considering that
134 competition over nest sites can be intense^{43,44}. Relationship tracking may also allow
135 individuals to notice if their partner is engaging in extra-pair copulations. Jackdaws are

136 typically considered to be sexually as well as socially monogamous^{45,46}, with studies to date
137 finding that extra-pair paternity is rare: it has been suggested that the high level of parental
138 investment required to successfully raise offspring may prevent birds from seeking extra-
139 pair copulations⁴⁶. However, recent findings suggest that extra-pair copulations may not be
140 as uncommon as previously thought⁴⁷; it may therefore pay females to track their partner's
141 behaviour.

142 Following the 'violation of expectation' paradigm employed in similar studies^{20,22,28}, we used
143 playback experiments to investigate whether female jackdaws respond to simulations of
144 male infidelity. During mating, including extra-pair copulations, male jackdaws give loud
145 copulation calls⁴⁸. In a recent study combining acoustic tracking and video surveillance, male
146 jackdaws were recorded emitting copulation calls at the same time as the female was alone
147 on the nest⁴⁷, suggesting that males do engage in extra-pair copulations and that this should
148 be an ecologically relevant stimulus for the female. Furthermore, in our study population,
149 intruder males are occasionally seen entering nest boxes and attempting to copulate with
150 the incubating female (*pers. obs.*). Although it is not yet known whether male copulation
151 calls encode information about caller identity, all other jackdaw vocalisations studied to
152 date have been shown to be individually distinct (food calls⁴⁹, contact calls⁵⁰ and alarm
153 calls⁵¹). Using playbacks of male contact calls and copulation calls in conjunction with female
154 contact calls, we simulated mating events occurring during the egg-laying period of the
155 breeding season, when copulation calls are heard most frequently in the colony (*pers. obs.*).
156 Contact calls were included to ensure that playback sequences simulated interactions
157 between individuals: contact calls are individually distinctive⁵⁰ and typically accompany
158 jackdaw copulation events. We used three playback treatments to test whether females
159 track changes in their own relationships and the relationships of other colony members. In

160 the 'Partner Incongruent' treatment, the playback simulated the focal female's partner
161 copulating with a female from a neighbouring nest, and this was expected to elicit a strong
162 response from the focal female. A 'Neighbour Incongruent' treatment was designed to test
163 third-party relationship recognition and simulated the male from a neighbouring nest
164 copulating with another female who was not their usual partner. This was predicted to elicit
165 an intermediate response from the focal female, as it violates expectations but does not
166 involve the focal female's own partner. Using a within-subjects design (Figure 1), the
167 responses of focal females to both 'Incongruent' playbacks were compared to a 'Congruent'
168 control predicted to elicit a neutral response (playback of a neighbouring male copulating
169 with their usual partner).

170 **Methods**

171 **Ethics Statement**

172 This experiment was carried out with approval from the University of Exeter research ethics
173 committee (2015/974) and following the ASAB Guidelines for the Treatment of Animals in
174 Behavioural Research and Teaching⁵². Although no birds were handled as part of this study,
175 subjects had been previously captured and ringed by qualified bird ringers licensed by the
176 British Trust for Ornithology and UK Home Office (project licence 30/3261).

177 **Study Population**

178 This experiment was conducted during the 2015-2017 breeding seasons using free-living
179 nest box populations of jackdaws, at three study sites in Cornwall, UK: a village churchyard
180 (Stithians 50°11'26"N, 5°10'51"W; 33 nest boxes), an active farmyard (Pencoose Farm

181 50°11'56"N, 5°10'9"W; 35 nest boxes), and at the University of Exeter's Penryn campus
182 (50°17'32"N; 5°11'96"W; 11 nest boxes).

183 **Playback Experiments**

184 *Audio Recordings*

185 Nest boxes occupied by breeding jackdaws were fitted with hidden CCTV cameras early in
186 the nest-building phase (late March-early April). A subset of nest boxes selected for this
187 experiment were also fitted with lapel microphones (n=30). Focal nest boxes were selected
188 with at least one marked individual, and with at least two nearby neighbouring pairs (within
189 50m). This was to ensure that neighbours' contact and copulation calls used in playbacks
190 would be familiar and ecologically relevant stimuli for the focal female.

191 Audio recordings were made early in the morning (start time: 0700-0900) during late March
192 and early April, when birds were engaged in nest building and copulation. Video recordings
193 were made with digital video recorders (JXD 990) and audio recordings made with
194 multitrack PCM recorders (Olympus LS-100 & Tascam DR-100MKII). Recordings were made
195 daily as required to obtain the necessary vocalisations for use in playback experiments. Each
196 recording ran for 3.5 hours. For some subjects, copulation and contact calls were extracted
197 from recordings obtained during previous seasons (2013-2015) using an identical protocol.

198 *Call extraction*

199 Clear exemplars of contact calls and copulation calls with minimal background noise were
200 extracted from nest box audio recordings and normalised for amplitude using Audacity
201 (www.audacityteam.org). The context of vocalisations and the identity of the caller were
202 ascertained using nest box videos collected alongside the audio recordings. In cases where

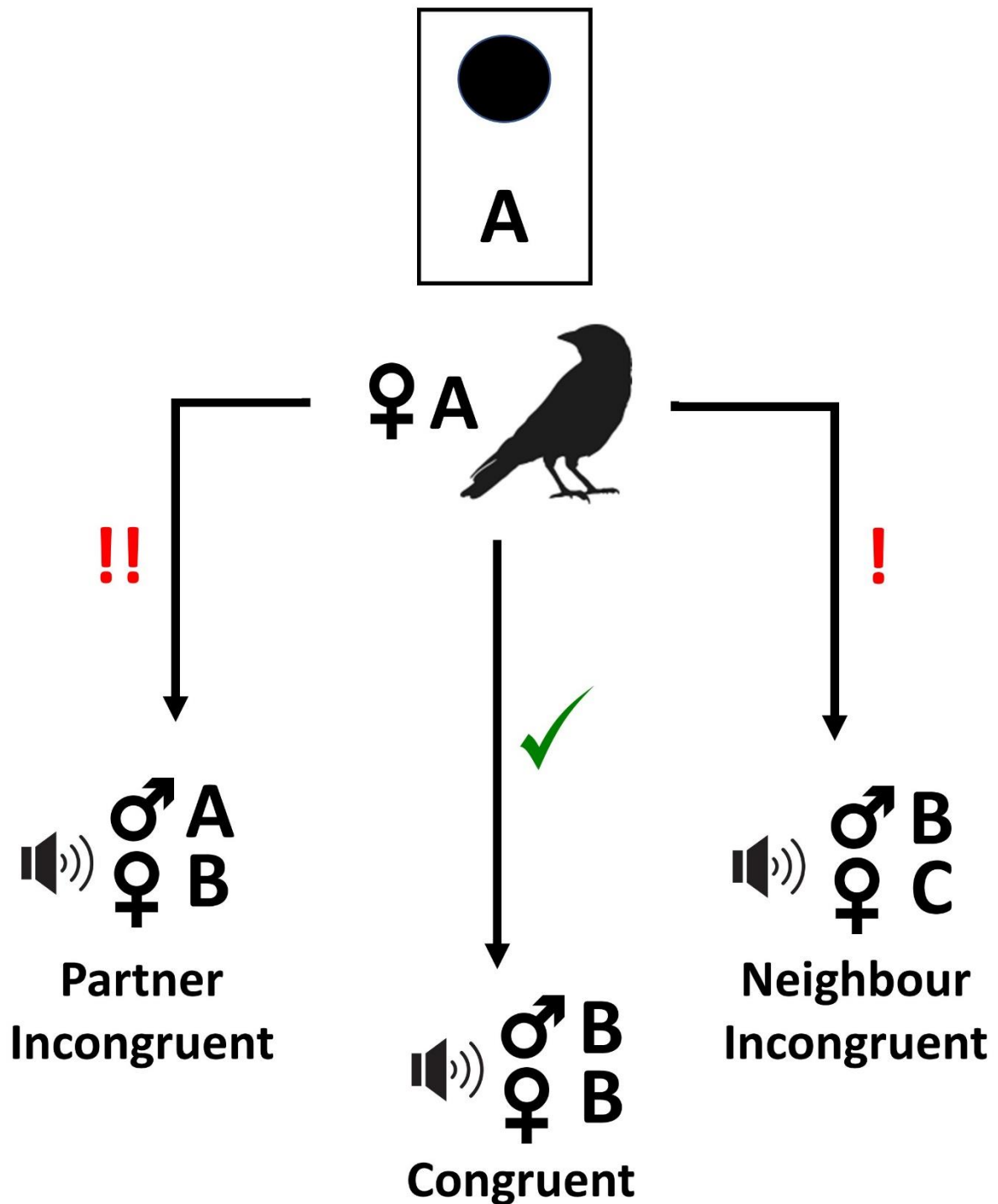
203 females vocalised during copulation, female calls were removed from the audio track,
204 leaving only the male copulation call. Extracted calls were arranged into playback files
205 containing a male contact call, followed by a female contact call, followed by a male
206 copulation call, to simulate a copulation event (see Figure S1 in supplementary material).
207 Calls occurred at 2s intervals to simulate natural calling, and male copulation calls varied in
208 length – this variation was retained to avoid excessively editing the acoustic stimulus and
209 potentially altering important aspects of call structure, but playback duration was later
210 controlled for statistically (see *Statistical Analysis*). Because of the limited number of
211 suitable copulation call recordings, and the variation in copulation call duration within and
212 between males, some copulation calls appeared in multiple playback trials. Focal females
213 heard the same copulation call from the male neighbour in the Congruent and Neighbour
214 Incongruent treatments, to ensure consistency across the experiment and minimise the
215 potential confounding effects of call duration. Contact calls were not repeated across
216 playback trials.

217 *Experimental Design*

218 This experiment followed a repeat measures design with each focal female (Female A) being
219 assigned three playback files (one for each of the experimental treatments) as follows:

- 220 • Congruent treatment: Neighbour Male B ‘copulating’ with Neighbour Female B.
- 221 • Partner incongruent treatment: Partner Male A ‘copulating’ with Neighbour Female
222 B.
- 223 • Neighbour incongruent treatment: Neighbour Male B ‘copulating’ with Neighbour
224 Female C (Figure 1).

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226

227 **Figure 1** Experimental setup for each nest box. The focal female from nest box A heard
 228 three playback presentations. In the 'Congruent' control treatment, focal female A heard a
 229 playback simulating a copulation event between the neighbouring male from nest box B and

230 the female from nest box B (his usual partner). The focal female (A) was expected to show a
231 weak response to this playback, denoted by a green tick mark. In the 'Neighbour
232 Incongruent' treatment, focal female A heard a playback simulating a copulation event
233 between the neighbouring male from nest box B and the female from nest box C (not his
234 usual partner). The focal female (A) was expected to show a stronger response to this
235 playback as it violated expectations, denoted by a red exclamation mark. In the 'Partner
236 Incongruent' treatment, the focal female (A) heard a playback simulating a copulation event
237 between her own partner (male from nest box A) with the neighbouring female from nest
238 box B. This playback was expected to elicit the strongest response from focal female A,
239 denoted by two red exclamation marks.

240 All experimental trials occurred soon after eggs were laid by the focal female, when females
241 were motivated to remain in the nest box but copulation calls were still being heard
242 frequently around the nesting colony. The order in which focal females received each
243 playback treatment was counterbalanced as far as possible, to ensure a matched design
244 across the experiment. At least 24 hours elapsed between trials for a given focal nest box.
245 All trials were carried out between 09:00 and 18:30, to coincide with peak activity times of
246 the birds⁴⁴.

247 We carried out 28 trials across three sites in 2015-2017, at 10 focal nest boxes (two trials
248 were discarded due to camera failure). This was the maximum sample size that could be
249 achieved in this case, due to the limited number of nest boxes with at least two close
250 neighbours and the difficulties in obtaining enough calls from these pairs. All females were
251 colour-ringed, except one bird whose partner was colour-ringed enabling identification of
252 individuals at the nest box. Trials were not carried out in the same area of the colony in the

253 same year. In cases where trials were carried out in the same area in subsequent years,
254 neighbouring birds from previous years were not included in the experiment as focal
255 individuals.

256 *Experimental trials*

257 Prior to trials, a remote-controlled FoxPro Fury 2 loudspeaker (disguised with vegetation to
258 avoid any neophobic responses) was attached to a tripod and placed approximately two-
259 thirds of the distance between the focal nest and the neighbour nest (mean distance 13.6m
260 between focal nest box and loudspeaker, range 8-21m). The loudspeaker was set up in the
261 same location for all trials at a nest box. Video recording equipment was also set up (DVR
262 JXD 990) to record female behaviour inside the focal nest box and neighbouring nest box.

263 Following setup, the experimenter returned to a concealed location a minimum of 50m
264 away. Playbacks only occurred after the focal female had remained undisturbed in the nest
265 box for at least 5 minutes (no disturbance outside the nest box, female had not left the box
266 or appeared at nest box entrance), and at least 5 minutes following the most recent visit by
267 the male. A baseline period of at least 20 minutes elapsed between the female's first return
268 to the nest box and presentation of the playback stimulus, to allow focal pairs to return to
269 normal behaviour after setting up equipment.

270 **Behavioural Analysis**

271 Footage of focal females was analysed using BORIS⁵³. The frequency and duration of
272 behaviours exhibited by the focal female were recorded for the 2-minute period following
273 the start of each playback presentation. These included: (i) categorical primary response to
274 playback (looking at the nest box entrance, peeking out of the nest box, or leaving the nest

275 box); (ii) time spent looking at the nest box entrance and peeking out of the nest box. All
276 playbacks were conducted at least 5 minutes after the last visit by the male. There were 5
277 instances where males returned to the nest box in the two minutes following the playback,
278 and in these cases all female behaviours occurring during and after the male's visit were
279 discounted.

280 Twenty percent of videos were analysed by a second coder who was blind to treatment.
281 Inter-rater reliability was analysed using a two-way intraclass correlation coefficient (ICC)
282 and indicated a high level of agreement between coders for all behaviours analysed (time
283 spent looking at entrance in the post-playback period: ICC=0.98, $p < 0.001$; time spent
284 peeking in the post-playback period: ICC=0.87, $p = 0.006$. In all cases, both coders agreed on
285 the categorical primary response to the playback).

286 **Statistical Analysis**

287 All analyses were carried out in R v3.4.3⁵⁴ with models were built using lme4⁵⁵ and ordinal⁵⁶.
288 Model plots were examined to ensure that assumptions were met (homogeneity and
289 normality of residuals), and minimum adequate models were obtained via log-likelihood
290 ratio tests.

291 *Behavioural response to playback*

292 In all cases females looked towards the entrance in response to the playback, but some
293 individuals subsequently went on to peek out of the nest box entrance or leave the nest
294 box. The extent of female response was analysed using a cumulative link mixed model
295 (CLMM) using female behaviour (LOOK/PEEK/EXIT) as an ordinal response term. In the
296 model, leaving the nest box was considered the strongest response to the playback (EXIT=3),

297 followed by peeking out of the nest box from a standing position (PEEK=2), with looking at
298 the nest box entrance from a seated position taken to be the weakest response (LOOK=1).
299 Treatment (congruent, partner incongruent or neighbour incongruent) and trial number (1-
300 3) were included as fixed effects and female ID as a random term. The effect of female
301 identity on response was analysed using log-likelihood comparison between the minimal
302 model and a cumulative link model without the random factor⁵⁷. Four trials were excluded
303 from the analysis as the male returned to the nest box prior to the end of the playback,
304 likely influencing female response.

305 *Time spent looking and peeking following playback*

306 For the two-minute period following the start of the playback, the time that each female
307 spent looking at the nest box entrance and/or peeking out of the nest box was analysed
308 using a general linear mixed model (GLMM) with a Gaussian error distribution. Treatment
309 (congruent, partner incongruent or neighbour incongruent), trial number (1-3) and length of
310 playback were included as fixed effects with focal female ID as a random term. Of the 28
311 trials, 6 were discarded as the male returned to the nest within two minutes of the
312 playback. One focal female responded to the playback by leaving the box immediately in all
313 three trials, and these were likewise excluded from the analysis. An influential data point
314 was also removed from the model following examination of Cook's distances: in this case,
315 the focal female spent the full two-minute period looking at the nest box entrance, but was
316 also facing the nest box entrance when the playback started (and therefore may not have
317 represented a reliable response to the playback).

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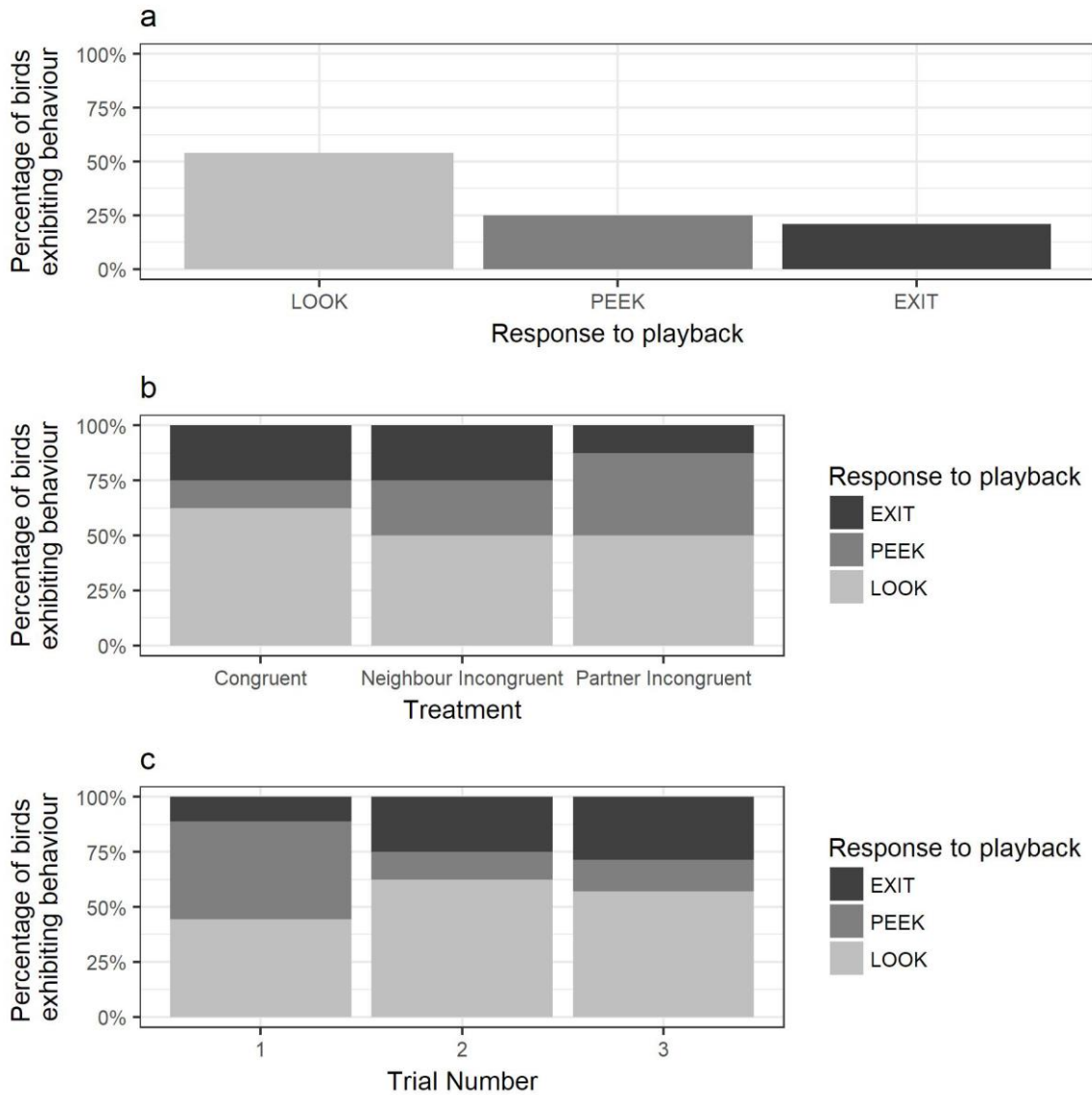
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320 **Results**

321 In all cases, females showed some form of response to the playback. These responses
322 ranged from looking at the nest box entrance from a seated position during incubation
323 (“LOOK”, 54% of cases), moving to look out of the nest box entrance (“PEEK”, 25% of cases)
324 and leaving the nest box (“EXIT”, 21% of cases) (see Figure 2). On no occasion did females
325 vocalise in response to the playback. During the post-playback observation period, there
326 were two occasions when an intruding male (not the focal female’s partner) entered the
327 nest box and attempted to copulate with the focal female. These incidents both occurred
328 during the first trial at the nest boxes in question and approximately half an hour after the
329 playback presentation; once following a ‘Partner Incongruent’ playback (2015) and once
330 following a ‘Congruent’ playback (2017). Intrusions by other males were not observed
331 during any other trials, either before or after the playback presentation.

332 **Behavioural response to playback**

333 Females responded to playbacks by looking at the nest box entrance (LOOK), peeking out of
334 the entrance from a standing position (PEEK) or leaving the nest box (EXIT). However, the
335 likelihood of females exhibiting these behaviours was similar across treatment groups
336 (CLMM: $X^2=1.21$, $df=2$, $p=0.55$) and was not influenced by trial order (CLMM: $X^2=0.40$, $df=2$,
337 $p=0.82$) (Figure 2, Table 1). Instead, response to playbacks was strongly influenced by the
338 identity of the female (CLM: $X^2=12.3$, $df=1$, $p<0.001$). For example, females that left the box
339 in one trial were more likely to do so in subsequent trials (Figure 3, Table 1).



340

341 **Figure 2** Barplots showing behavioural responses of females to playback treatments: looking

342 at the nest box entrance from an incubating position (LOOK, light grey bars); peaking out of

343 the nest box entrance from a standing position (PEEK, mid-grey bars), and leaving the nest

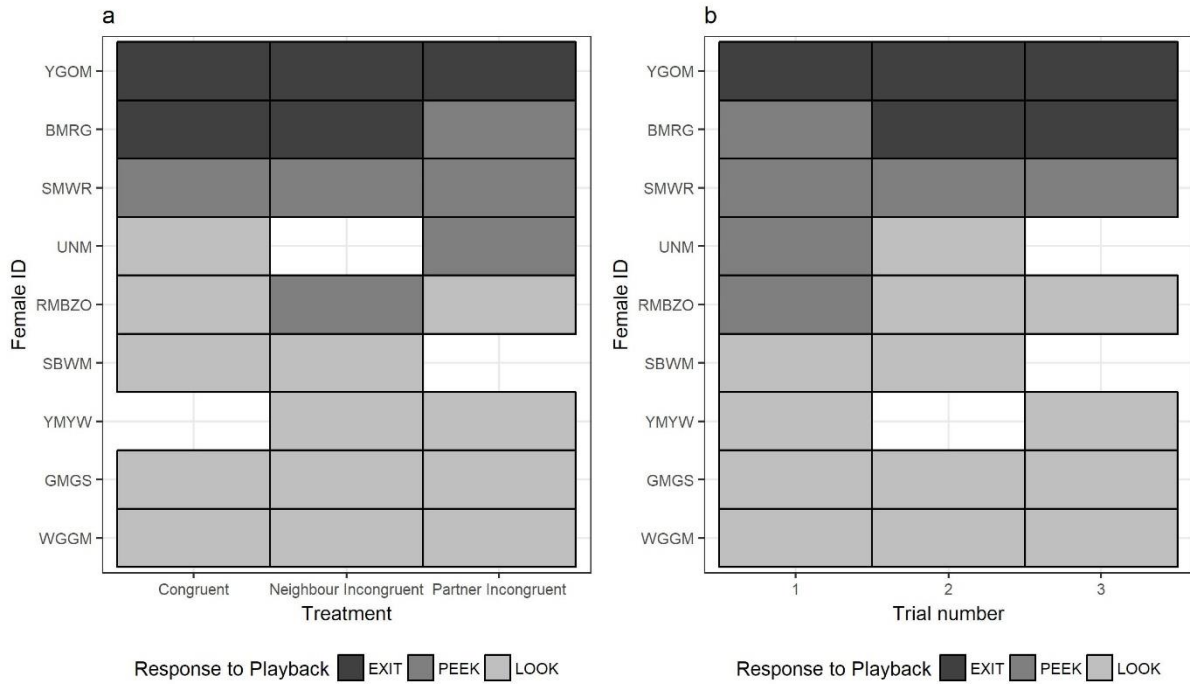
344 box (EXIT, dark grey bars). a) Percentage of females exhibiting each response across all

345 trials; b) percentage of females exhibiting each behaviour by treatment (congruent,

346 neighbour incongruent, partner incongruent); c) percentage of females exhibiting each

347 behaviour by trial number (1-3, treatment presentations counterbalanced across trials).

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349

350 **Figure 3** Tile plots showing responses of focal females to the three playbacks, according to
 351 a) treatment (Congruent, Neighbour Incongruent, Partner Incongruent) and b) trial number
 352 (1-3). Female ID (y-axis) shows colour-ring combinations of focal females. Tile colour
 353 corresponds to the behavioural response of the female to the playback: looking at the nest
 354 box entrance from an incubating position (LOOK, light grey bars); peeking out of the nest
 355 box entrance from a standing position (PEEK, mid-grey bars), and leaving the nest box (EXIT,
 356 dark grey bars). Blank tiles represent trials where a reliable measure of females' initial
 357 response to the playback could not be obtained.

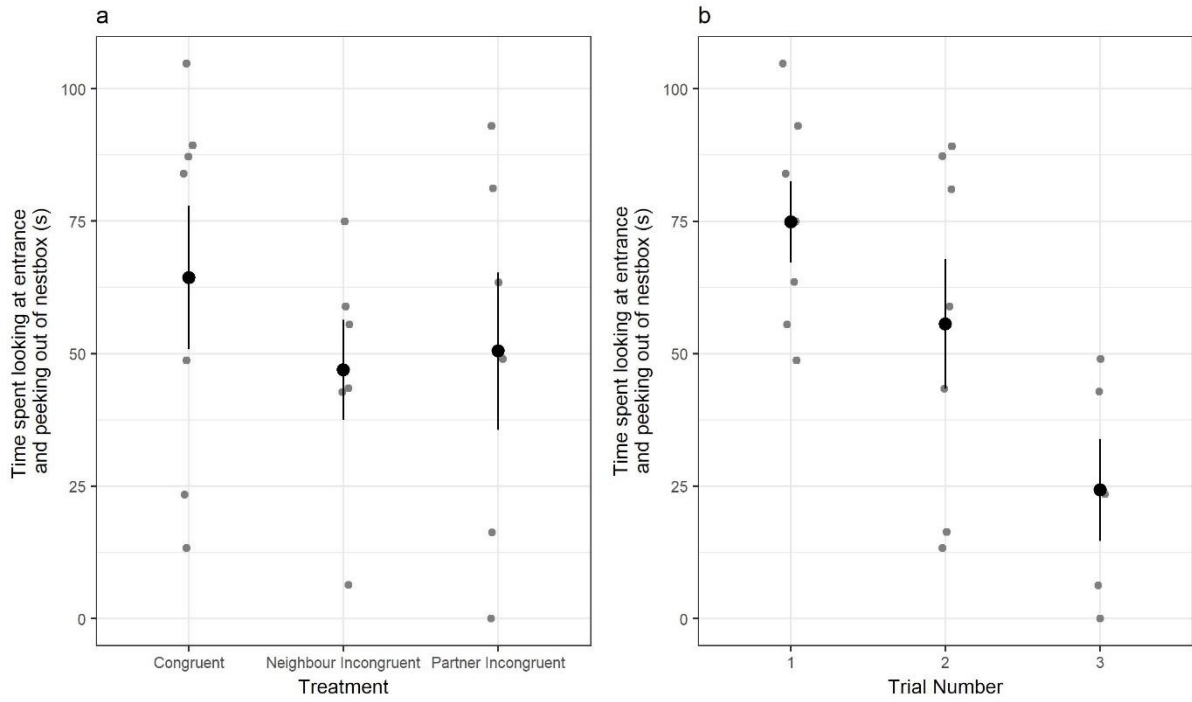
358 **Table 1** Output of CLMM investigating the effect of treatment (congruent, neighbour
 359 incongruent, partner incongruent) and trial number (1-3) on the ordinal response of females
 360 to the playback (LOOK=looking at nest box entrance, PEEK=peeking out of nest box
 361 entrance, EXIT=leaving the nest box). Congruent treatment and Trial 1 are the reference
 362 levels, n=24 observations of 9 females. Values shown from full model, statistically significant
 363 effects are given in italics.

Model parameters	β	SE	z-value	p-value
Threshold (response)				
LOOK PEEK	1.47	2.74	0.54	
PEEK EXIT	6.31	2.74	2.30	
Treatment				
Congruent (reference)				
Neighbour incongruent	1.56	1.80	0.86	0.39
Partner incongruent	-0.13	1.63	-0.08	0.94
Trial number				
Trial 1 (reference)				
Trial 2	-0.53	1.62	-0.33	0.74
Trial 3	-0.22	1.66	-0.13	0.89
Random effects			Variance	SE
<i>Female ID</i>			31.89	5.65

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365 **Time spent looking/peeking following playback**

366 In the two-minutes following the start of the playback, females spent an average of 54s
367 ($\pm 7.3s$) either looking at or peeking out of the nest box entrance. The length of time that
368 females spent looking at or out of the nest box entrance did not differ between treatments
369 (GLMM: $X^2=0.58$, $df=2$, $p=0.75$), and was not influenced by the duration of the playback
370 (GLMM: $X^2=1.12$, $df=1$, $p=0.29$). However, females spent less time looking and peeking
371 following playbacks as trials progressed (GLMM: $X^2=10.13$, $df=2$, $p=0.006$) (Figure 4, Table
372 2).



373

374 **Figure 4** Plots showing the time spent by focal females looking at the nest box entrance or
 375 peeking out of the nest box entrance in the two minutes post-playback, by a) treatment
 376 (congruent, neighbour incongruent, partner incongruent) and b) trial number (1-3). Grey
 377 points represent individual data points (n=19 observations of 8 females), and black points
 378 with error bars denote mean and standard error.

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386 **Table 2** Output of GLMM investigating time spent looking at nest box entrance and peeking
 387 out of nest box entrance in the two minutes following the start of playback. Full model
 388 includes treatment, trial order and playback duration as fixed effects (statistically significant
 389 effects given in italics). Congruent treatment and Trial 1 are the reference levels, n=19
 390 observations of 8 females.

	Fixed effect		β	SE	t-value
Full model					
	Intercept		101.46	22.97	4.42
	Treatment	Congruent (reference)			
		Neighbour incongruent	-7.27	13.0	-0.56
		Partner incongruent	-9.59	13.12	-0.73
	<i>Trial order</i>	<i>Trial 1 (reference)</i>			
		<i>Trial 2</i>	-16.72	12.31	-1.36
		<i>Trial 3</i>	-47.20	13.55	-3.48
	Playback duration		-1.33	1.24	-1.08

391

392 **Discussion**

393 We found no effect of treatment on jackdaws' responses to playbacks, with females
 394 behaving in a similar manner following simulations of their partner's infidelity, their
 395 neighbour's infidelity and a congruent control. There were no significant differences in
 396 females' initial response (looking at the nest box entrance, peeking out of the nest box
 397 entrance or leaving the nest box) or the duration of the response (time spent looking at, or
 398 out of, the nest box entrance). However, females appear to habituate to playbacks over
 399 time, as the length of time females spent investigating the stimulus (looking at or out of the
 400 nest box entrance) decreased over successive trials.

401 Each subject's initial response to the playback (looking at the nest box entrance, peeking out
402 of the nest box entrance or leaving the nest box) was strongly influenced by the identity of
403 the individual. Inter-individual variation between females was significant, with females'
404 response during their first trial strongly predicting their response during subsequent trials,
405 regardless of treatment. In terms of the duration of this response (time spent looking at/out
406 of the nest box entrance), none of the test subjects behaved as predicted: we found no
407 evidence of a stronger response to the 'Partner Incongruent' or 'Neighbour Incongruent'
408 treatments compared to the 'Congruent' control. Two females looked/peeked for longer
409 following the infidelity simulation of their partner compared to the control playback, but
410 this may be because these subjects heard their partner's infidelity simulation first. Overall,
411 these results suggest that individual variation likely plays an important role in influencing
412 subjects' responses in these types of experiments, yet these individual differences are rarely
413 examined or discussed explicitly in studies of cognition⁵⁸⁻⁶⁰.

414 Although these results do not provide any evidence that jackdaws track their own
415 relationships and the relationships of others in their social group, this does not necessarily
416 imply that jackdaws are incapable of third-party relationship recognition. Instead, it may be
417 that birds simply failed to demonstrate this ability within the context of our experimental
418 setup. The fact that females failed to respond to simulations of their own partner's
419 infidelity, as well as the infidelity of a male neighbour, is consistent with this possibility.

420 There are several potential explanations as to why female responses did not differ between
421 experimental treatments. Firstly, the experiment was carried out during an ecologically
422 relevant period when birds were copulating at a high rate compared to other stages in the
423 breeding attempt. It may be that if copulation calls are heard frequently around the colonies
424 at this time, individuals attend to (or ignore) all copulation calls equally. Moreover, it is

425 possible that females do not discriminate between the copulation calls of individual males
426 (although jackdaw contact calls are individually distinct⁵⁰, and were included in playback
427 sequences to simulate interactions between individuals). Furthermore, if extra-pair
428 copulations are extremely rare^{45,46}, females may not perceive the playback stimulus as an
429 'infidelity'. However, recent evidence⁴⁷ and observations of intruder males in our own study
430 population suggest that extra-pair copulations in jackdaws may occur more commonly than
431 previously thought. For this reason, it seems that it would be beneficial for females to notice
432 when their partner is copulating with another female. If females do perceive the playback
433 stimulus as an 'infidelity', perhaps there is no advantage to females in acting on this
434 information (e.g. by leaving the nest to gather more information, or to retaliate against their
435 unfaithful partner⁶¹). In a similar experiment, Crockford et al.²⁸ found that subordinate male
436 baboons respond to playbacks of female copulation calls that were indicative of a recent
437 consortship having ended, as these cues provide highly relevant information which may
438 allow them to gain 'sneaky' matings. In our study it is possible that, if there is no direct
439 fitness benefit to females, the social information indicating male infidelity is not attended to
440 or acted upon to the same extent. The fact that nest intrusions occurred following two of
441 the playback presentations (where another male entered the focal nest box and attempted
442 to copulate with the resident female) raises the possibility that male jackdaws may
443 eavesdrop on copulation events in a similar way to baboons²⁸. Finally, if male infidelity does
444 not reduce subsequent paternal care, there may be little cost to their female partner. Given
445 the high degree of social monogamy in this species⁴⁶, it may be that male extra-pair
446 copulation does not merit a response from females. It would be interesting to determine
447 whether male extra-pair copulation behaviour, or playback simulations of male infidelity,
448 influence female behaviour over the long term (e.g. in terms of mate choice, see ⁶²).

449 Females showed habituation to playbacks over time, suggesting that there may be aspects
450 of our experimental setup that were incongruent with naturally-occurring copulation
451 events. For example, the timings of calls in the playback sequence may not be a reliable
452 indication of two birds being in close proximity at the same time. Each playback sequence
453 consisted of a male contact call and female contact call, followed by a copulation call from
454 the same male (Figure S1 in supplementary material). A pause of two seconds occurred
455 between each call, which represents natural calling rates for individual birds (unpublished
456 data). Playbacks were conducted when the area was quiet and no other birds were heard
457 calling, but in busy areas of the colony where calling is generally frequent, it may be that the
458 calls of multiple birds are frequently heard together without any direct interaction between
459 callers. The fact that all playback calls were emitted from the same direction may have
460 provided an additional cue that calls represent a social interaction; on the other hand, call
461 direction may be difficult for a female jackdaw to discern from inside a nest box.

462 Observations of female responses to naturally-occurring copulation events and male
463 infidelity may shed light on why females failed to respond to our playbacks, and would be an
464 important avenue for future study.

465 It could be that jackdaws are more likely to respond to relationship changes that influence
466 agonistic encounters, such as changes in dominance rank. Jackdaw colonies are structured
467 according to a linear dominance hierarchy, where females assume the rank of their male
468 partner⁴². Pairs then compete for food and nest sites, with conflict over nesting cavities
469 being particularly intense^{43,44}. Recognising changes in dominance rank may be of fitness
470 relevance to birds in allowing them to gain access to resources whilst avoiding conflicts that
471 are potentially costly. Playback experiments have demonstrated that primates recognise
472 changes in dominance rank^{19,20}, and hyenas also appear to apply knowledge of third-party

473 relationships during agonistic interactions²⁴ (but fail to demonstrate this ability in other
474 contexts³²). Unfortunately, jackdaws do not give dominance calls, which would make an
475 experimental test of knowledge of third-party ranks logistically challenging. Other corvids
476 have been shown to respond to simulated changes in dominance rank, both within their
477 own social group and a neighbouring group²². However, this study was conducted in
478 captivity with small groups of birds housed in close proximity. Birds therefore had extensive
479 opportunities to learn about social relationships by observing frequent interactions between
480 all group members; it is currently unknown whether these opportunities occur similarly
481 under natural conditions. Therefore, the extent of third-party relationships knowledge in
482 the wild, and the contexts in which corvids apply this knowledge, remains to be determined.

483 This study presents one of the first experimental tests of third-party relationship recognition
484 in a non-primate under natural conditions. To date, only one other field experiment has
485 been conducted on birds, and suggests that acorn woodpeckers are aware of which
486 individuals make up neighbouring groups⁴¹. However, it is unclear whether the act of calling
487 together in woodpeckers provides any information about the nature of the dyadic
488 relationship between callers. Here, we used copulation calls, which are directed at specific
489 individuals during a specific type of social interaction, to investigate dyadic and third-party
490 relationship representation. We found no evidence that jackdaws track their own
491 relationships and the relationships of other individuals in their social group. However, we
492 cannot rule out that jackdaws possess this ability, as none of the test subjects responded in
493 a manner consistent with the experimental predictions. Moreover, due to the difficulties in
494 obtaining a sufficient number of calls from close neighbours in the experimental colonies,
495 our sample size (n=10) is modest (see Methods). Our sample size is in line with similar
496 studies of corvids in captivity, both for tests of social cognition and cognitive abilities more

497 generally^{22,63-67}. It could be that under natural conditions, where subjects' attention is
498 divided and there are more confounding environmental variables, larger sample sizes are
499 required to detect an effect. This emphasises the need to complement research in the
500 laboratory with rigorous field studies addressing questions related to social cognition.

501 A growing body of research, both observational and experimental, shows that species that
502 live in complex societies possess knowledge of third-party relationships and other socio-
503 cognitive abilities considered to be relatively 'sophisticated'. To date, many of these studies
504 have been carried out using captive populations, with field studies mostly confined to
505 primates. More studies are needed in a wider range of species and social systems, especially
506 in a field context where findings may be more likely to accurately reflect the cognitive
507 processes animals use to solve real-world socio-ecological challenges^{39,40}. Studies of this
508 kind would make a valuable contribution to our understanding of social cognition in
509 different species, and how these abilities help individuals to navigate a changing social
510 world.

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519

520 **Author Contributions**

521 V.E.L. and A.T. designed the experiment; V.E.L. ran the experimental trials and analysed the
522 data; G.E.M. provided logistical support and maintained field sites/study populations; V.E.L.
523 and A.T. wrote the manuscript.

524 **Data Availability**

525 Data and R scripts associated with this study are available in the Figshare repository (DOI:
526 10.6084/m9.figshare.7825943).

527 **Competing interests**

528 The authors declare no competing interests.

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