

1 **Jackdaw nestlings can discriminate between conspecific calls but do not beg**  
2 **specifically to their parents**

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15 **Running title:** Vocal discrimination by jackdaw nestlings

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24 The ability to recognize other individuals may provide substantial benefits to young  
25 birds, allowing them to target their begging efforts appropriately, follow care-givers  
26 after fledging and establish social relationships later in life. Individual recognition using  
27 vocal cues is likely to play an important role in the social lives of birds such as corvids  
28 that provision their young post-fledging and form stable social bonds, but the early  
29 development of vocal recognition has received little attention. We used playback  
30 experiments on jackdaws, a colonial corvid species, to test whether nestlings begin to  
31 recognize their parents' calls before fledging. Although the food calls made by adults  
32 when provisioning nestlings were individually distinctive, nestlings did not beg  
33 preferentially to their parents' calls. Ten day-old nestlings not only responded equally to  
34 the calls of their parents, neighboring jackdaws whose calls they were likely to overhear  
35 regularly and unfamiliar jackdaws from distant nest-boxes, but also to the calls of rooks,  
36 a sympatric corvid species. Responses to rooks declined substantially with age, but 20  
37 and 28 day-old nestlings were still equally likely to produce vocal and postural begging  
38 responses to parental and non-parental calls. This is unlikely to be due to an inability to  
39 discriminate between calls, as older nestlings did respond more quickly and with greater  
40 vocal intensity to familiar calls, with some indication of discrimination between parents  
41 and neighbors. These results suggest that jackdaws develop the perceptual and cognitive  
42 resources to discriminate between conspecific calls before fledging but may not benefit  
43 from selective begging responses.

44

45 **Keywords:** begging; Corvidae; *Corvus monedula*; food calls; parental care; social  
46 cognition; vocal recognition

47 **INTRODUCTION**

48

49 Many social animal species possess mechanisms for parents and offspring to recognize  
50 one another. Among birds and mammals, recognition often relies on vocal cues, which  
51 can travel over long distances and serve as reliable indicators of identity, provided that  
52 they are individually distinctive and remain relatively stable over time (Beer 1971). For  
53 parents, recognition of offspring's vocalizations can be crucial in preventing mis-  
54 directed parental care if offspring are mobile or found in communal nests or crèches.  
55 Bank swallows (*Riparia riparia*), for example, use their chicks' begging calls to locate  
56 them among hordes of other colony members (Beecher, Beecher, and Hahn 1981).  
57 Offspring too may use vocalizations to discriminate between their parents and other  
58 adults. A classic example is that of king penguins (*Aptenodytes patagonicus*), where  
59 vocal recognition is essential for hungry chicks to locate their parents among hundreds  
60 of conspecifics (Aubin and Jouventin 1998).

61

62 In many bird species, parents produce distinctive food calls when they arrive with food  
63 for their young, causing chicks to respond by begging (Leonard, Fernandez, and Brown  
64 1997; Madden, Kilner, and Davies 2005). Food calls have been shown to be  
65 individually distinctive in a number of species (Lessells, Rowe, and McGregor 1995;  
66 McDonald et al. 2007), but few studies have tested whether young respond specifically  
67 to the food calls of their own parents. Signal detection theory suggests that the degree of  
68 specificity in receivers' responses will be determined by the balance between the costs  
69 of responding to inappropriate signals and failing to respond to genuine signals and thus  
70 missing critical feeding opportunities (Wiley 2006). Very young birds may have poorly

71 developed sensory and cognitive systems, so may not yet be capable of reliable fine-  
72 scale discrimination, leading them to respond unselectively to noises near the nest  
73 (Leonard, Horn, and Mukhida 2005; Dor et al. 2006). As they become better able to  
74 discriminate, chicks may stand to benefit by begging only in response to their own  
75 parents' calls. Such selective responses may help to minimize the energetic or growth  
76 costs of begging (Kilner 2001; Rodríguez-Gironés, Zuniga, and Redondo 2001; but see  
77 Moreno-Rueda 2006) and the risk attracting the attention of predators (McDonald,  
78 Wilson, and Evans 2009; Haff and Magrath 2011) or aggressive conspecifics (Beecher,  
79 Beecher, and Hahn 1981; Proffitt and McLean 1991; Insley 2001). In species where  
80 parents continue to care for mobile young, the benefits to offspring of selective  
81 responses to parental calls may increase further as the time to leave the nest approaches.  
82 Ancient murrelets (*Synthliboramphus antiquus*) for instance are highly precocious, and  
83 mutual parent-offspring recognition is apparent from the age of two days after hatching,  
84 when nestlings begin to leave their nest (Jones, Falls, and Gaston 1987). In contrast,  
85 cavity-nesting Galah cockatoo (*Cacatua roseicapilla*) chicks do not begin responding  
86 selectively to their parents' calls until 40 days of age, six days before they fledge and  
87 join a crèche with fledglings from other broods (Rowley 1980).

88

89 In addition to its role in parent-offspring communication, the ability to recognize others'  
90 voices may provide important benefits in establishing and maintaining social  
91 relationships after offspring become independent (Wanker et al. 1998; Cheney and  
92 Seyfarth 2007). Among birds, corvids typically exhibit complex societies with stable  
93 individualized relationships and show behaviors in which vocal recognition has been  
94 implicated in primates (Whiten and Byrne 1988; Cheney and Seyfarth 2007), including

95 mutual support (Seed, Clayton, and Emery 2007; Fraser and Bugnyar 2010), alliance  
96 formation (Lorenz 1952; Emery et al. 2007; Loretto, Fraser, and Bugnyar 2012) and  
97 deception (Bugnyar and Kotrschal 2002; Clayton, Dally, and Emery 2007; Grodzinski  
98 and Clayton 2010). A handful of studies have demonstrated that corvids use  
99 individually distinctive calls to discriminate between conspecifics (pinyon jays,  
100 *Gymnorhinus cyanocephalus*, Marzluff 1988; rooks, *Corvus frugilegus*, Røskaft and  
101 Espmark 1984; jungle crows, *Corvus macrorhynchos*, Kondo, Izawa, and Watanabe  
102 2012; ravens, *Corvus corax*, Boeckle and Bugnyar 2012), but the development of this  
103 ability has received little attention. In the only test of vocal discrimination by corvid  
104 chicks, McArthur (1982) showed that pinyon jay nestlings respond more strongly to  
105 their parents' food calls than to those of other adults during the week prior to fledging,  
106 but the responses of younger chicks were not investigated. No study has yet examined  
107 when individual vocal recognition emerges during nestling development. Further  
108 research into the development of vocal recognition is thus critical for our understanding  
109 of parent-offspring communication and the emergence of later socio-cognitive abilities  
110 in corvids.

111

112 We used playback experiments to investigate the development of vocal recognition in a  
113 nest-box population of wild jackdaws (*Corvus monedula*). Jackdaws are an ideal species  
114 to examine this issue as both parents contribute extensively to offspring provisioning  
115 (Henderson and Hart 1993), announcing their feeding visits with characteristic food  
116 calls (Goodwin 1986; Cramp and Perrins 1994), and because young jackdaws may  
117 receive numerous benefits for being able to discriminate conspecific calls, both at the  
118 nestling stage and later in life. Jackdaws are cavity-nesters and breed colonially, so

119 nestlings may benefit from recognizing their parents' calls and not wasting time and  
120 energy begging in responding to calls of other adults nearby. Keeping quiet unless a  
121 parental visit is certain may also avoid attracting the attention of predators and  
122 aggressive conspecifics that may attack chicks in attempts to take over the nest cavity  
123 (Röell 1978; author's unpublished data). The benefits of vocal recognition may increase  
124 further as the time for fledging approaches at around 30-35 days after hatching. During  
125 the first six weeks post-fledging, juveniles remain dependent on parents for food and  
126 follow them in response to food calls (Cramp and Perrins 1994). Shortly afterwards,  
127 juveniles begin to form individualized relationships with non-parents and establish  
128 dominance hierarchies (Röell 1978; Henderson, Hart, and Burke 2000; von Bayern et al.  
129 2007), so the ability to recognize individuals and track their relationships could provide  
130 major benefits (Röell 1978; Emery et al. 2007). Finally, jackdaws emit regular  
131 vocalizations both while foraging and in flight, which may allow them to keep in close  
132 proximity to partners even when flying among hundreds of other individuals (Jolles et  
133 al. 2013). One might therefore expect that these birds have the ability to use individual  
134 vocal recognition to identify and coordinate movements with social partners in  
135 adulthood.

136

137 We tested whether parental food calls were individually distinct and whether nestlings  
138 at different stages of development differed in their begging responses to the food calls  
139 of their own parents versus those of other adult jackdaws. To test whether nestlings  
140 would respond to any familiar adult food call, we played back food calls of parents,  
141 neighboring adults from a nearby nest-box (whose calls the focal nestlings were likely  
142 to overhear regularly) and stranger adults from a distant nest-box. We also examined

143 whether nestlings responded indiscriminately to other sympatric birds by playing calls  
144 of rooks, *Corvus frugilegus*, another corvid species found throughout the year in the  
145 vicinity of the nest-box population. As young nestlings sometimes begged in response  
146 to the sound of human observers near nest-boxes, we expected ten day-old chicks to  
147 respond equally to all playbacks. However, as nestlings' sensory and cognitive  
148 capacities developed and the time for fledging approached, we predicted that 20-28 day-  
149 old nestlings would start to discriminate between calls and beg specifically in response  
150 to their own parents' calls

151

## 152 **METHODS**

### 153 **Study Population**

154 This work was conducted on a jackdaw nest-box population comprising 140 nest-boxes,  
155 of which 69 were occupied by breeding pairs, arranged in 15 discrete sites in and around  
156 the village of Madingley, Cambridgeshire, United Kingdom, during the 2012 breeding  
157 season (14 April - 13 June 2012). A small proportion of the jackdaw population was  
158 ringed for individual identification under a license from the British Trust for  
159 Ornithology (45 ringed adults, of which eight occupied our nest boxes). We equipped  
160 20 nest-boxes that were occupied by breeding jackdaws with a CMOS IR nest-box  
161 camera and an AKG C417 PP tie-clip microphone hidden behind a panel in the top of  
162 the nest-boxes, out of sight of the occupants. We made video recordings with a digital  
163 video recorder (Mini HDVR LS-H720) and audio recordings with Marantz PMD600  
164 and Olympus LS-100 PCM recorders, recording 16 bit files at a sampling rate of 48  
165 KHz. On days 5, 8 and 22 after the first chick hatched we made audio and video

166 recordings of parental vocalizations and behaviors inside the nest-box for ca. 3.5 hours  
167 between 7 and 11am. Rook calls were recorded in local rookeries during the breeding  
168 season using a Sennheiser ME66/K6 directional microphone placed in the middle of the  
169 rookery. The rookeries used for these recordings were all located at a distance of at least  
170 100 m from the nearest nest-box site, but rooks moved throughout the study area so all  
171 nestlings would be exposed to rook calls on a regular basis.

172

### 173 **Playback Experiments**

174 From the audio recordings of each nest-box we selected clear exemplars of parental  
175 food calls with minimal background noise, and normalized the amplitude of all audio  
176 clips using Adobe Audition 3.0 (Adobe Systems Inc., San Jose, CA, U.S.A.). In the  
177 majority of cases it was not possible to determine with certainty whether food calls were  
178 made by the male or female parent, so our playbacks differentiate between nests, but not  
179 between sexes. For every nest-box and nestling age group (days 10, 20 and 28 post-  
180 hatching), we made playback files containing three different calls for each of four  
181 treatments: (i) parents, (ii) neighbor jackdaws from the same nest-box site (<40m from  
182 focal nest-box; range 11-39m); (iii) stranger jackdaws from a different nest-box site  
183 (>120m from focal nest-box; range 120-908m) and (iv) rooks (>100 m from focal nest-  
184 box). Jackdaws show hatching asynchrony and high nestling mortality, especially  
185 among later-hatched chicks (Cramp et al. 1994). Mean brood size ( $\pm$  SE) in  
186 experimental nest-boxes was  $1.88 \pm 0.16$  chicks at day 10;  $1.5 \pm 0.13$  chicks at day 20;  
187 and  $1.47 \pm 0.13$  chicks at day 28. Of the 20 nest-boxes originally fitted with cameras  
188 and microphones, we ran playbacks on 16 nests that had surviving chicks on day 10.  
189 Four of these nests lost their broods to naturally occurring mortality before day 20. To



190 compensate, we added a further four nest-boxes to the experiment to maintain a sample  
191 size of 16 nests for playbacks on day 20. One additional box was used in the experiment  
192 on day 28, giving a total of 21 nest-boxes used throughout the course of the experiment  
193 (final sample sizes per age category were  $N = 16$  nest-boxes on days 10 and 20 and  $N =$   
194  $17$  on day 28). We were unable to run the “neighbor” playback treatment at some nest-  
195 boxes as they did not have breeding neighbors (number of nest-boxes without neighbors  
196  $= 2$  at day 10;  $1$  at days 20 and 28). To avoid pseudo-replication (Kroodsma 1989), we  
197 used different calls for each playback trial, such that the tested chicks never heard the  
198 same call more than once, and none of the calls were used more than once across the  
199 entire experiment. There were only five exceptions where we did not record sufficient  
200 numbers of parental food calls, forcing us to use the same call as a playback stimulus  
201 twice, but we played this call at different focal nest-boxes. As every call recording  
202 contained some ambient noise, we inserted the calls into a playback file with similar  
203 ambient noise extracted from our recordings. The ambient noise was faded in for 20s at  
204 the start of the playback file and faded out for 20s at the end, with 30s of ambient noise  
205 in between the three calls, so each playback treatment lasted 100s in total.

206

207 We played the playback files in an uncondensed WAV format to chicks in the nest-box  
208 from an iPod Mini connected to a high-fidelity Vifa D26 NC-05-06 neodymium tweeter  
209 speaker (commonly used in avian playback experiments; see Larsen and Dabelsteen  
210 1997) and a Kemo 12v amplifier. The speaker was attached to a pole of length 4m and  
211 held in front of the nest-box out of the line of sight of the nestlings. Playback amplitude  
212 was calibrated prior to the experiment by recording calls played from the speaker in  
213 front of an unoccupied nest-box to determine the amplitude that matched that in

214 recordings of naturally occurring parental calls. Both the amplitude and the distance  
215 between the speaker and the nest-box opening (0.5m) were standardized across all  
216 playback trials. To reduce the potential for habituation to playbacks, there was a break  
217 of 15 minutes between the playbacks of the different treatments. The playback order of  
218 the different treatments was randomized across nest-boxes and nestling age groups. All  
219 playbacks were performed between 10.00 and 15.30 hr. During each playback trial we  
220 recorded chicks' responses with the same audio and video recorders in the nest-box as  
221 were used for the initial recordings of the parental calls. All work adhered to the  
222 Association for the Study of Animal Behaviour's guidelines for the use of animals in  
223 research.

224

## 225 **Statistical Analyses**

226

### 227 **Distinctiveness of adult food calls**

228 To test whether parental food calls were individually distinctive, we analyzed food calls  
229 made by birds whose identity was known. It was often difficult to determine which  
230 parent made a given food call recorded at a nest-box, but in a minority cases we could  
231 identify calling individuals with certainty from video records through visible leg rings  
232 or behavioral observations. We were able to isolate clean calls with no audible  
233 background noise for eight known individuals, obtaining eight calls per individual,  
234 produced during different feeding visits and, where possible, on different days. To  
235 compare these calls, we generated spectrograms of calls (window length: 2.67 ms;  
236 frequency resolution: 188 Hz) and then ran a spectrographic cross correlation (SPCC)

237 with the batch spectrogram correlation function in Raven Pro 1.4 acoustic analysis  
238 software (Cornell Lab Of Ornithology, USA). Rather than restricting comparisons to a  
239 predetermined and potentially incomplete set of variables, SPCC analysis compares all  
240 the measurable spectral features of two calls over time by ‘sliding’ them past each other  
241 and obtaining the peak correlation score, generating a matrix of correlation coefficients  
242 between 0 and 1 for all possible pairwise comparisons (Clark, Marler, and Beeman  
243 1987). To test the hypothesis that the correlation value within individuals is greater than  
244 the correlation between individuals, we used a procedure based on the Mantel test. We  
245 compared the SPCC matrix to a second ‘hypothesis matrix’ containing a binary code,  
246 with ‘1’s representing within-individual comparisons and ‘0’s representing between-  
247 individual comparisons in the equivalent positions. A significant positive correlation  
248 between the SPCC correlation matrix and the hypothetical matrix indicates that the  
249 within-individual correlation values are higher than the between-individual values  
250 (Sharp and Hatchwell 2005). To check whether subtle similarities in in background  
251 noise within nest-boxes could be responsible for apparent within-individual similarity in  
252 calls, we also ran a similar analysis based on SPCC comparisons of the 1s of  
253 background noise preceding all calls.

254

### 255 **Nestling responses**

256 To make maximal use of the data, we analyzed all possible responses to every playback  
257 call (four treatments, with three calls per treatment, giving a maximum of 12 potential  
258 chick responses per nest-box for each age category) using multifactorial analyses. We  
259 used generalized estimating equations (GEE) for ordinal response terms and linear  
260 mixed models (LMMs) or generalized linear mixed models (GLMMs) for normal or

261 non-normal data respectively. Nest-box identity was fitted as a random factor to control  
262 for repeated measures in all models. Chick age (10, 20 or 28 days) and playback  
263 treatment (parent, neighbor, stranger or rook), were fitted as explanatory terms, along  
264 with call order (first, second or third call in each playback treatment) and the number of  
265 chicks in the nest. As disturbance at the nest may have deterred parents from visiting  
266 during the experiment, leading to changes in chicks' hunger levels and begging  
267 responses, treatment order (first, second, third or fourth playback treatment) was fitted  
268 as an additional explanatory term. We initially included all explanatory terms in the  
269 models. All possible two-way interactions between them were investigated and terms  
270 were sequentially dropped until the minimal model contained only significant terms  
271 remained in the model. Probability values for significant terms were derived from this  
272 minimal model, while values for non-significant terms were obtained by adding each  
273 term individually to the minimal model (Crawley 2002). Model residuals were visually  
274 inspected to ensure homogeneity of variance, normality of error and linearity. Post hoc  
275 analyses of differences between levels of interest within categorical variables were  
276 conducted by sequentially excluding levels from models to enable comparisons of the  
277 remaining category levels. Wald statistics ( $\chi^2$ ) for models with non-normal response  
278 terms are quoted with numerator degrees of freedom for each explanatory term; for  
279 LMM models with normal response terms we quote F statistics with numerator and  
280 denominator degrees of freedom, separated by a comma. Means are quoted  $\pm$  SE  
281 throughout. Tables of results for all multifactorial analyses including all effect sizes and  
282 SEs are provided in the supplementary material. The total sample size for full analyses  
283 was  $N = 21$  nest-boxes across all age categories (for analyses within age categories,  $N =$

284 16 on days 10 and 28;  $N = 17$  on day 28). All analyses were conducted in Genstat 16.1  
285 (VSN International) except where otherwise specified.

286

### 287 **Nestling postural responses**

288 From the nest-box videos, we scored the intensity of the maximum postural responses  
289 seen amongst the nestlings to each playback call, from 1 (no response at all) to 6 (full  
290 begging response: body and neck fully extended, with open gape; see Table S1 in  
291 supplementary material). A response score of 0 was included for cases where the chick  
292 quickly covered down (typically in the far corner of the nest-box) in response to the  
293 call. 15% of videos were analysed by a second coder blind to experimental treatments  
294 (inter-observer reliability:  $Kappa = 0.87$ ;  $P < 0.001$ ). Postural responses were analyzed  
295 using a GEE with ordinal logistic method and an exchangeable correlation structure in  
296 SPSS (version 20, IBM Corp). Nest-box was fitted as the subject variable to control for  
297 repeated measures.

298

### 299 **Probability of vocal response**

300 We examined chicks' tendencies to produce begging calls in response to playbacks  
301 using a GLMM with a binomial (1,0) response term indicating whether or not any chick  
302 in the brood produced a vocal response to each playback call.

303

### 304 **Characteristics of vocal response**

305 Subtle differences in vocal response features may provide evidence for vocal  
306 discrimination that is not apparent by examining vocal response probability or postural  
307 responses alone (Boeckle and Bugnyar 2012). We therefore used LMMs to analyse

308 chicks' latency to respond to broadcast calls and the total duration of chick begging,  
309 focusing specifically on responses to conspecific food calls. We also used the Choose  
310 Measurements tool in Raven Pro 1.4 to extract from the spectrograms (measured with  
311 window length: 2.67 ms; frequency resolution: 188 Hz) a number of acoustic  
312 parameters that reflect the intensity of vocal responses: peak amplitude (dimensionless  
313 sample units, u), root-mean-square (RMS) or "effective" amplitude (u), total energy  
314 (dB), peak frequency (Hz), peak power (dB) and average power (dB) of the first call. As  
315 these parameters show substantial auto-correlation, we used principal components  
316 analyses (PCA) with a varimax rotation to obtain composite measures of vocal begging  
317 intensity, using a minimum eigenvalue of 1.0 to determine the number of components  
318 extracted from the PCA. We then used the rotated scores from each component as  
319 response variables in LMM analyses with nest-box as a random term to control for  
320 repeated measures. Initial analyses showed that variables loaded differently on principal  
321 components at different ages, so we conducted separate analyses on PCA scores for  
322 playbacks at days 10, 20 and 28. As it was not possible to determine which nestling in a  
323 brood was calling, total brood responses were used as the units of analysis.

324

## 325 **RESULTS**

### 326 **Distinctiveness of adult food calls**

327 Jackdaws produce food calls of short duration (range: 88-179 ms) with a peak frequency  
328 between 937.5 and 5438 Hz ( $N = 64$ ; Figure 1). Rook calls are acoustically different  
329 from jackdaw calls, with a longer duration of 390-814 ms and peak frequency of 1378-  
330 2067 Hz ( $N = 24$ ; Figure 1). SPCC analyses of jackdaw call structure showed that calls

331 from the same individual were more similar in acoustic structure than calls from  
332 different individuals (mean correlation coefficient within individuals =  $0.53 \pm 0.01$ ;  
333 between individuals =  $0.35 \pm 0.003$ ). A Mantel test confirmed that within- and between-  
334 individual correlation coefficients were significantly different (10000 permutations,  $r =$   
335  $0.35$ ,  $P < 0.005$ ), indicating that jackdaw food calls are individually distinctive. Within-  
336 individual call similarity could not be an artefact of background noise, as a Mantel test  
337 revealed no significant difference in SPCC values of background noise from recordings  
338 within and between individuals (10000 permutations,  $r = 0.05$ ,  $P = 0.11$ ).

339

#### 340 **Nestling postural responses**

341 There was a significant interaction between age and playback treatment, with nestlings  
342 of 10 days of age responding equally to all treatments whereas older nestlings showed  
343 significantly reduced responses to rook calls compared to conspecific calls (Figure 2A-  
344 C; GEE; age\*treatment:  $\chi^2_6 = 16.56$ ;  $P < 0.011$ ; Table S2). Restricting the analysis to 10  
345 day-old nestlings confirmed there was no effect of treatment at this age (GEE:  $\chi^2_3 =$   
346  $0.125$ ;  $P = 0.989$ ). GEE analysis restricted to older nestlings showed a significant effect  
347 of treatment, with lower responses to rook than jackdaw calls (GEE:  $\chi^2_3 = 22.95$ ;  $P =$   
348  $< 0.001$ ). Excluding responses to rooks from this analysis, nestlings responded with  
349 similar intensity to all jackdaw treatments (GEE:  $\chi^2_2 = 0.49$ ,  $P = 0.783$ ).

350

#### 351 **Probability of vocal response**

352 GLMM analysis of whether or not nestlings begged in response to calls revealed a  
353 significant interaction between nestling age and playback treatment (Figure 2D-E;

354 GLMM:  $\chi^2_6 = 24.74$ ;  $P < 0.001$ ; Table S3), controlling for the effect of treatment order  
355 ( $\chi^2_3 = 11.88$ ;  $P < 0.008$ ). Restricting the GLMM analysis to 10 day-old nestlings showed  
356 no significant difference in response to any of the different treatments ( $\chi^2_3 = 1.20$ ;  $P =$   
357  $0.753$ ). On days 20 and 28 there was a significant effect of treatment, with nestlings  
358 being less likely to respond to rooks than to conspecific calls (GLMM on 20 and 28  
359 day-old nestlings; effect of treatment:  $\chi^2_3 = 40.44$ ;  $P < 0.001$ ). However, they did not  
360 respond significantly differently to the three categories of jackdaw calls: excluding  
361 responses to rooks from GLMM there was no significant difference in responses to  
362 jackdaw call treatments ( $\chi^2_2 = 3.26$ ,  $P = 0.196$ ).

363

#### 364 **Characteristics of vocal responses**

365 In cases when nestlings responded vocally to jackdaw food calls (i.e. excluding cases  
366 with no vocal response), the duration of begging calls declined as chicks grew older  
367 (LMM:  $F_{2,201} = 20.05$ ;  $P < 0.001$ ; Table S4), but was unaffected by playback treatment  
368 (treatment;  $F_{2,195} = 0.54$ ;  $P = 0.582$ ; treatment\*age:  $F_{4,188} = 4.55$ ;  $P = 0.287$ ). In contrast,  
369 analysis of nestlings' latency to beg revealed a significant interaction between age and  
370 treatment (Figure 3A-C; LMM: age\*latency  $F_{4,188} = 2.42$ ;  $P = 0.050$ ; Table S5; response  
371 variable normalized for analyses with a Box-Cox transformation). LMM analyses  
372 within age groups showed no significant differences between treatments at age 10 ( $F_{2,38}$   
373  $= 0.67$ ;  $P = 0.519$ ) but at age 20 there was a significant effect of treatment ( $F_{2,89} = 4.77$ ;  
374  $P = 0.011$ ). Sequentially excluding treatment levels from the LMM revealed that chicks  
375 were significantly faster to respond to parents than to both neighbors ( $F_{1,51} = 8.75$ ;  $P =$   
376  $0.005$ ) and strangers ( $F_{1,52} = 4.45$ ,  $P = 0.044$ ). At day 28 there was a marginally non-



377 significant effect of treatment (LMM;  $F_{2,50} = 3.10$ ;  $P = 0.054$ ), with faster responses to  
378 parents and neighbors than to strangers.

379

380 All PCAs on acoustic parameters yielded two principal components, with PC1  
381 explaining 61-77% and PC2 16-21% of the variance in the data across the three age  
382 categories. Scores from these components were unrelated to playback treatment on day  
383 10 (LMMs; PC1:  $F_{2,38} = 0.13$ ;  $P = 0.879$ ; PC2:  $F_{2,38} = 0.83$ ;  $P = 0.444$ ) or 20 (PC1:  
384  $F_{2,83} = 0.16$ ;  $P = 0.857$ ; PC2:  $F_{2,83} = 1.08$ ;  $P = 0.344$ ). For begging calls produced on day  
385 28, however, PC1 scores differed significantly between treatments, (Figure 3D-E;  
386 LMM:  $F_{2,52} = 14.68$ ;  $P < 0.001$ ; Table S6). At this age, peak amplitude, peak power and  
387 energy all had high loadings on PC1 (see Table S7 for rotated loadings of variables on  
388 each extracted component). Sequentially removing treatment levels from the LMM  
389 analysis revealed that PC1 scores were significantly higher in response to parents and  
390 neighbors than to strangers (parents vs. strangers:  $F_{1,39} = 20.96$ ;  $P < 0.001$ ; neighbors vs.  
391 strangers:  $F_{1,30} = 12.55$ ;  $P < 0.001$ ) but responses to parents and neighbors did not differ  
392 ( $F_{1,32} = 0.09$ ;  $P = 0.765$ ). PC2 scores did not differ between treatments ( $F_{2,53} = 0.82$ ;  $P =$   
393 0.449).

394

## 395 **DISCUSSION**

396 In this study we showed that the food calls of jackdaws, like jackdaw contact calls  
397 (Wascher et al. 2012) and the calls of several other corvid species (Marzluff 1988;  
398 Kondo, Izawa, and Watanabe 2010; Boeckle, Szpl, and Bugnyar 2012) are individually  
399 distinctive and could thus, in principle, be used for individual recognition. Nestlings

400 responded to playbacks with vocal and postural begging displays, suggesting that  
401 jackdaw food calls serve to stimulate begging prior to provisioning, presumably  
402 improving the efficiency of food transfers from parents to offspring as occurs in other  
403 bird species (Leonard et al. 1997; Madden et al. 2005). Ten day-old nestlings responded  
404 indiscriminately to all broadcast calls, but began to discriminate between the calls of  
405 their own species and those of other sympatric corvids as they grew older, all but  
406 eliminating their responses to rook calls by the age of 28 days post-hatching. However,  
407 nestlings were no more likely to respond to their parents' food calls than to those of  
408 neighboring and unfamiliar conspecifics. Nevertheless, examination of the temporal and  
409 acoustic characteristics of vocal begging responses provided some evidence that  
410 nestlings may in fact be capable of discriminating between conspecific calls.

411

412 Given evidence that indiscriminate begging can entail substantial costs (Kilner 2001;  
413 Rodríguez-Gironés, Enquist, and Lachmann 2001; Haff and Magrath 2011), we  
414 expected jackdaw nestlings to beg specifically in response to their parents' calls.  
415 Analyses of whether or not nestlings begged in response to calls and the strength of  
416 their postural responses provided no support for this prediction. During the first days  
417 after hatching, nestlings often begged in response to noises in the environment,  
418 including the sound of human observers walking past the nest-box or placing a ladder  
419 against the tree, and 10 day-old nestlings showed no discrimination in their responses to  
420 conspecific or heterospecific calls. It remains to be determined whether chicks'  
421 indiscriminate responses at this age are due to sensory or cognitive constraints (Dor et  
422 al. 2006), or because they have not yet learned the relation between jackdaw calls and  
423 food (cf. Raihani & Ridley 2008). In contrast to younger chicks, nestlings of 20 and 28

424 days of age were less likely to beg vocally and showed reduced postural displays to  
425 rook than jackdaw calls. However, contrary to our expectations, there were no  
426 differences in the probability of vocal begging or the intensity of postural responses to  
427 parental, neighbor or stranger jackdaw food calls. It is possible that if chicks  
428 discriminate only between adult calls of a particular sex then our playbacks, which did  
429 not differentiate between male and female calls, may have failed to detect any  
430 differences. However, given that both parents play a major role in chick provisioning,  
431 this possibility seems unlikely. Instead, our results seem to suggest two possibilities:  
432 either nestlings are unable to recognize parental calls and so cannot respond  
433 differentially, or they are capable of discriminating between calls, but do not derive  
434 sufficient benefits to merit selective responses.

435

436 Analyses of the latency and acoustic intensity of nestlings' vocal responses provide  
437 some support for the latter possibility. While ten-day old chicks responded equally  
438 quickly to all broadcast jackdaw calls, 20 day-old chicks were significantly faster to  
439 respond to their parents' calls than to those of strangers, with a smaller but significant  
440 difference (at the 5% level) between responses to parents and neighbors. There was a  
441 trend for a similar pattern on day 28, with faster responses to parents and neighbors than  
442 to strangers, though this effect just failed to reach significance. Comparisons of the  
443 intensity of vocal responses using composite Principal Component scores provided  
444 further evidence for discrimination. Here, significant effects were apparent only on day  
445 28, when nestlings showed significantly stronger responses to parents and neighbors  
446 than to strangers. The effect sizes for these results are relatively small and must be  
447 interpreted with caution, but taken together the consistent pattern of results suggests that

448 jackdaw nestlings may in fact be capable of distinguishing between conspecific calls  
449 prior to fledging. Faster responses to parents than to neighbors on day 20 provide some  
450 indication that nestlings may perceive differences in these calls, both of which are likely  
451 to be familiar and heard on a daily basis. However, other results show differences only  
452 between strangers and the two familiar call categories. We therefore tentatively suggest  
453 that jackdaw chicks can at least discriminate between familiar and unfamiliar calls.

454

455 Together our results suggest that while jackdaws may develop the perceptual and  
456 cognitive resources to distinguish between conspecific calls while in the nest, they may  
457 derive few benefits from selectively limiting their begging responses by discriminating  
458 between the calls of parents and other adults. The principal costs of indiscriminate  
459 begging are likely to be the time and energy costs of unrewarded begging displays and  
460 the risks of attracting predators or aggressive conspecifics (Kilner 2001; Haff and  
461 Magrath 2011). However, jackdaw nestlings may substantially reduce many of these  
462 costs by ceasing to beg to non-jackdaw noises in the environment without needing to  
463 discriminate further between conspecific calls. Moreover, as chicks grew older their  
464 greater size and ability to sit upright, which was evident from nest-box video  
465 recordings, may have enabled them to look through the cavity entrance to see parents  
466 arriving with food. Consequently, nestlings in the final days before fledging may have  
467 been less reliant than younger chicks on food calls to stimulate begging, which could  
468 help explain the overall reduction in responsiveness to food calls from day 20 to 28.  
469 Finally, although we and others have recorded instances of nest predation and  
470 intraspecific attacks, these events appear to be rather rare (Röell 1978; Gibbons 1987).  
471 At our study site, we have observed a single (non-lethal) conspecific attack on a

472 nestling. Most suspected instances of nest predation at our study site occurred when  
473 entire broods disappeared overnight, suggesting that the culprits may have been  
474 nocturnal predators, rather than diurnal predators that might be attracted by chick  
475 begging (author's unpublished data). Thus, for jackdaw nestlings the costs of begging  
476 may be insufficient to warrant highly selective responses to parents. Our results contrast  
477 with findings from other species living in similar conditions, in which nestlings do show  
478 vocal recognition of their parents' calls. For example, galah cockatoos, like jackdaws,  
479 are cavity nesters and nestlings have been shown to respond preferentially to their  
480 parents' calls a week or so before fledging (Rowley 1980). Similar results were found  
481 for nestling pinyon jays, a gregarious corvid species (McArthur 1982). Both pinyon jays  
482 and galah cockatoos live in fission-fusion societies similar to those of jackdaws, but  
483 differences in discrimination by nestlings may be explained by differences in the  
484 relative costs of individual begging, for instance if jackdaw nestlings are under  
485 relatively lower risk of predation.

486

487 Previous studies of offspring-parent vocal recognition in birds have tended to rely on  
488 gross response measures such as the presence or absence of a response or categorical  
489 measures of chick posture and movements towards speakers (Beer 1971; Rowley 1980;  
490 McArthur 1982; Storey et al. 1992; Aubin and Jouventin 1998). Our work indicates that  
491 detailed examination of vocal response characteristics may reveal discriminatory  
492 abilities that would not otherwise be apparent. In jackdaws, subtle differences in the  
493 latency and vocal intensity of nestling responses may reflect the early emergence of a  
494 skill that is likely to be critical later in life when fledglings must follow their parents  
495 and form social relationships. Post-fledging experiments, such as a preference test in

496 which fledglings are presented with calls from two different individuals simultaneously,  
497 may shed more light on the development of individual recognition in this species.  
498 Comparative experiments between species may allow us to elucidate the causes of  
499 variation in the development of vocal recognition. Furthermore, despite several reports  
500 of individual vocal recognition in captive corvids (Røskaft & Espmark 1984; Kondo et  
501 al. 2012; Boeckle & Bugnyar 2012), little is known about how corvids employ vocal  
502 recognition in their natural environments (but see Marzluff 1988). Studies of vocal  
503 recognition in the wild will provide further insights into the mechanisms underlying the  
504 sophisticated socio-cognitive skills for which corvids are well known (Emery and  
505 Clayton 2004).

506

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508

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633 **FIGURE LEGENDS**

634 **Figure 1.** Sound spectrogram of a jackdaw feeding call (left) and a rook call (right).

635 Produced in Syrinx ([www.syrinxpc.com](http://www.syrinxpc.com)) with 512-point fast Fourier transform (FFT)

636 and a Blackman window (no filter applied).

637

638 **Figure 2.** (A-C) Postural response intensity scores and (D-E) probability of vocal

639 responses to the different playback treatments at three nestling ages: 10 days (A, D), 20

640 days (B, E) and 28 days (C, F) post-hatching. P = parents, N = neighboring jackdaws, S

641 = stranger jackdaws, R = rooks. Means  $\pm$  SE calculated from raw data are used for

642 visual representation of postural scores. Values for vocal probability responses are

643 derived from GLMMs in Table S3. \*\*\* indicates that among 20 and 28 day-old chicks

644 there was a significant effect of treatment only when responses to rook calls are

645 included in the model ( $P < 0.001$ ; Tables S2 and S3).

646

647 **Figure 3.** Characteristics of nestlings' vocal responses to conspecific food calls. Panels

648 show (A-C) latency to respond and (D-E) intensity of vocal response from principal

649 component scores on day 10 (A, D), 20 (B, E) and 28 (C, F). P = parents, N =

650 neighboring jackdaws, S = stranger jackdaws. Significance levels in pairwise

651 comparisons derived by excluding factor levels from LMM analysis: \*\*\* $P < 0.001$ ; \*\*

652  $P < 0.01$ ; \*  $P < 0.05$ . Bars show predicted means  $\pm$  SE from LMMs in Tables S5 and

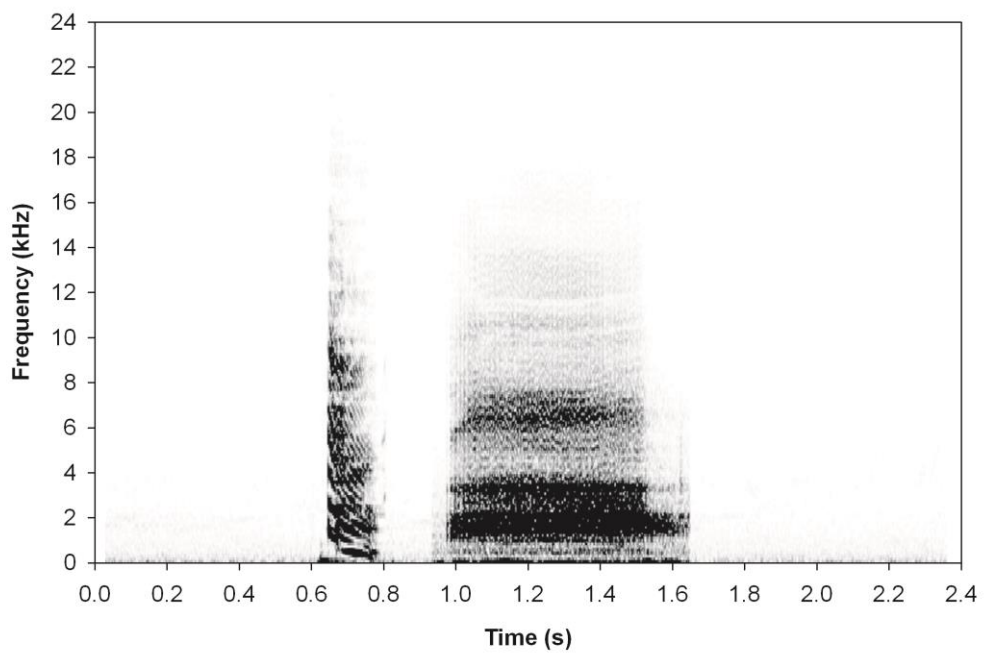
653 S6.

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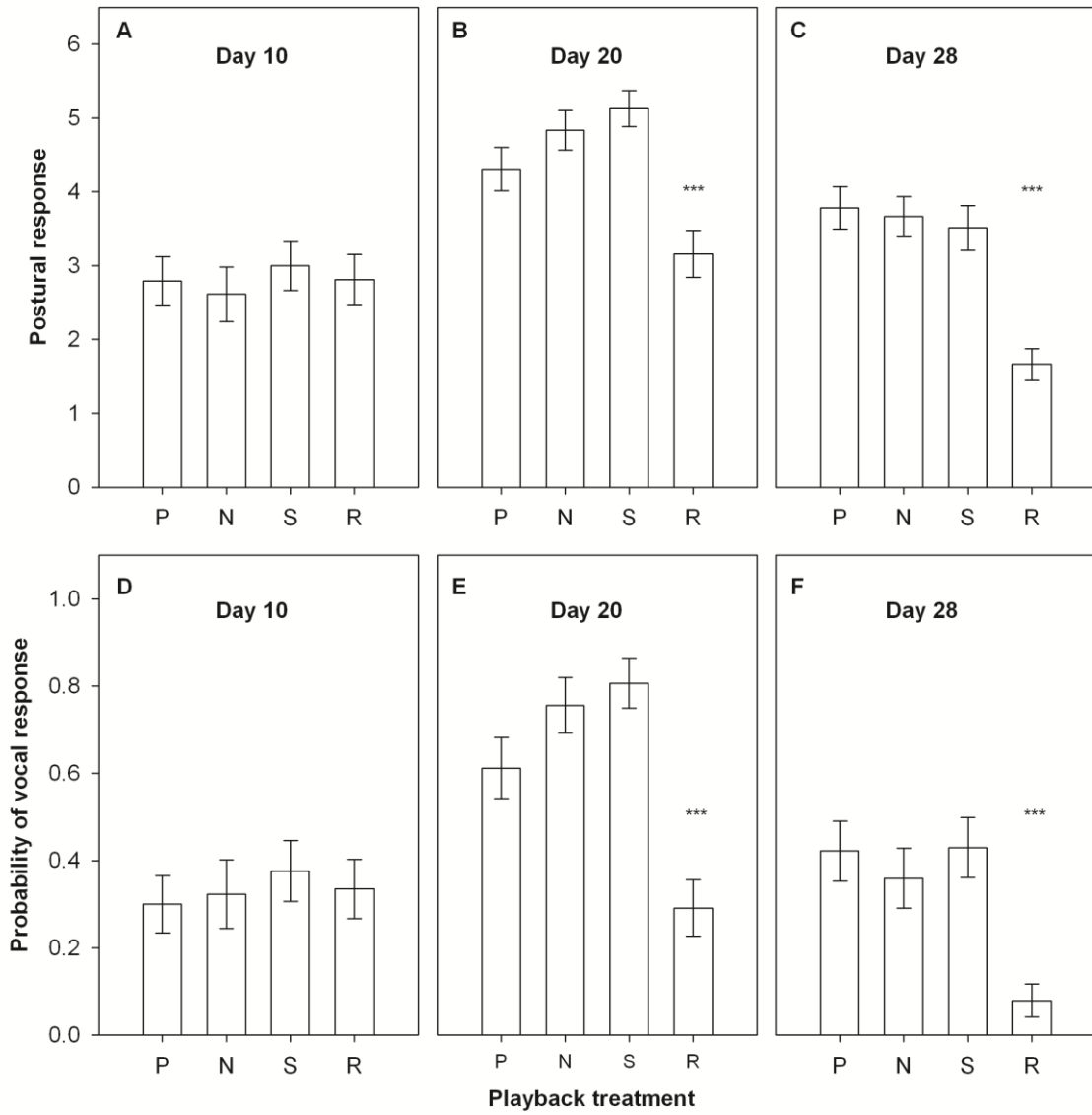
657 Figure 1



658

659

660 Figure 2



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662

