1 **Jackdaw nestlings can discriminate between conspecific calls but do not beg**

2 **specifically to their parents**

3 Lies Zandberg [a,b], Jolle W. Jolles, [a, c], Neeltje J. Boogert [d] & Alex Thornton[a,e]*

4 a Department of Psychology, University of Cambridge

5 b Department of Animal Sciences, Behavioural Ecology Group, Wageningen University

6 c Department of Zoology, University of Cambridge

7 d School of Psychology and Neuroscience, University of St Andrews

8 e Centre for Ecology and Conservation, University of Exeter, Cornwall Campus

9

10 * Correspondence: Alex Thornton, Centre for Ecology and Conservation, University of

11 Exeter, Penryn Campus, Penryn, Cornwall TR10 9EZ

12 Email: alex.thornton@exeter.ac.uk

13 Tel: +44(0)1326 255081

14

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

16

17

18

19

20

21

22

23

The ability to recognize other individuals may provide substantial benefits to young

birds, allowing them to target their begging efforts appropriately, follow care-givers

after fledging and establish social relationships later in life. Individual recognition using

vocal cues is likely to play an important role in the social lives of birds such as corvids

that provision their young post-fledging and form stable social bonds, but the early

development of vocal recognition has received little attention. We used playback

experiments on jackdaws, a colonial corvid species, to test whether nestlings begin to

recognize their parents' calls before fledging. Although the food calls made by adults

when provisioning nestlings were individually distinctive, nestlings did not beg

preferentially to their parents' calls. Ten day-old nestlings not only responded equally to

the calls of their parents, neighboring jackdaws whose calls they were likely to overhear

regularly and unfamiliar jackdaws from distant nest-boxes, but also to the calls of rooks,

a sympatric corvid species. Responses to rooks declined substantially with age, but 20

and 28 day-old nestlings were still equally likely to produce vocal and postural begging

responses to parental and non-parental calls. This is unlikely to be due to an inability to

discriminate between calls, as older nestlings did respond more quickly and with greater

vocal intensity to familiar calls, with some indication of discrimination between parents

and neighbors. These results suggest that jackdaws develop the perceptual and cognitive

resources to discriminate between conspecific calls before fledging but may not benefit

from selective begging responses.

INTRODUCTION

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

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

whether nestlings responded indiscriminately to other sympatric birds by playing calls

of rooks, *Corvus frugilegus*, another corvid species found throughout the year in the

vicinity of the nest-box population. As young nestlings sometimes begged in response

to the sound of human observers near nest-boxes, we expected ten day-old chicks to

respond equally to all playbacks. However, as nestlings' sensory and cognitive

capacities developed and the time for fledging approached, we predicted that 20-28 day-

old nestlings would start to discriminate between calls and beg specifically in response

to their own parents' calls

METHODS

Study Population

This work was conducted on a jackdaw nest-box population comprising 140 nest-boxes,

of which 69 were occupied by breeding pairs, arranged in 15 discrete sites in and around

the village of Madingley, Cambridgeshire, United Kingdom, during the 2012 breeding

season (14 April - 13 June 2012). A small proportion of the jackdaw population was

ringed for individual identification under a license from the British Trust for

Ornithology (45 ringed adults, of which eight occupied our nest boxes). We equipped

20 nest-boxes that were occupied by breeding jackdaws with a CMOS IR nest-box

camera and an AKG C417 PP tie-clip microphone hidden behind a panel in the top of

the nest-boxes, out of sight of the occupants. We made video recordings with a digital

video recorder (Mini HDVR LS-H720) and audio recordings with Marantz PMD600

and Olympus LS-100 PCM recorders, recording 16 bit files at a sampling rate of 48

KHz. On days 5, 8 and 22 after the first chick hatched we made audio and video

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

Playback Experiments

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

recordings of naturally occurring parental calls. Both the amplitude and the distance

between the speaker and the nest-box opening (0.5m) were standardized across all

playback trials. To reduce the potential for habituation to playbacks, there was a break

of 15 minutes between the playbacks of the different treatments. The playback order of

the different treatments was randomized across nest-boxes and nestling age groups. All

playbacks were performed between 10.00 and 15.30 hr. During each playback trial we

recorded chicks' responses with the same audio and video recorders in the nest-box as

were used for the initial recordings of the parental calls. All work adhered to the

Association for the Study of Animal Behaviour's guidelines for the use of animals in

research.

Statistical Analyses

Distinctiveness of adult food calls

To test whether parental food calls were individually distinctive, we analyzed food calls

made by birds whose identity was known. It was often difficult to determine which

parent made a given food call recorded at a nest-box, but in a minority cases we could

identify calling individuals with certainty from video records through visible leg rings

or behavioral observations. We were able to isolate clean calls with no audible

background noise for eight known individuals, obtaining eight calls per individual,

produced during different feeding visits and, where possible, on different days. To

compare these calls, we generated spectrograms of calls (window length: 2.67 ms;

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 (χ^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 cowered 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

13

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 ± 0.01;

333   between individuals = 0.35 ± 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-

16

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, Szipl, and Bugnyar 2012) are individually

399 distinctive and could thus, in principle, be used for individual recognition. Nestlings

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

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

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

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

507 **ACKNOWLEDGEMENTS**

508

515

516

517 **REFERENCES**

518 Aubin T, Jouventin P. 1998. Cocktail-party effect in king penguin colonies. Proc R Soc

519 B 265:1665–1673.

520   Beecher MD, Beecher IM, Hahn S. 1981. Parent-offspring recognition in bank swallows

521   (*Riparia riparia*): II. development and acoustic basis. Anim Behav 29:95–101.

522   Beer C. 1971. Individual recognition of voice in the social behavior of birds. Adv Stud

523   Behav 3:27–74.

524   Boeckle M, Bugnyar T. 2012. Long-term memory for affiliates in ravens. Curr Biol

525   22:801–806.

526   Boeckle M, Szipl G, Bugnyar T. 2012. Who wants food? Individual characteristics in

527   raven yells. Anim Behav 84:1123–1130.

528   Bugnyar T, Kotrschal K. 2002. Observational learning and the raiding of food caches in

529   ravens, *Corvus corax*: is it "tactical" deception? Anim Behav 64:185–195.

530   Cheney DL, Seyfarth RM. 2007. Baboon metaphysics: the evolution of a social mind.

531   Chicago: University of Chicago Press.

532   Clark CW, Marler P, Beeman K. 1987. Quantitative analysis of animal vocal

533   phonology: an application to swamp sparrow song. Ethol 76:101–115.

534   Clayton NS, Dally JM, Emery NJ. 2007. Social cognition by food-caching corvids. The

535   western scrub-jay as a natural psychologist. Phil Trans R Soc B 362:507–22.

536   Cramp S, Perrins C. 1994. Handbook of the birds of Europe, the Middle East and North

537   Africa. The birds of the Western Palearctic. Crows to finches, vol. VIII. Oxford: Oxford

538   University Press.

539   Crawley MJ. 2002. Statistical computing. Chichester, U.K.: John Wiley & Sons, Ltd.

540   Dor R, Kedar H, Winkler DW, Lotem A. 2006. Begging in the absence of parents: a

541   "quick on the trigger" strategy to minimize costly misses. Behav Ecol 18:97–102.

542   Emery NJ, Clayton NS. 2004. The mentality of crows: convergent evolution of

543   intelligence in crows and apes. Science 306:1903–1907.

544   Emery NJ, Seed AM, von Bayern AMP, Clayton NS. 2007. Cognitive adaptations of

545   social bonding in birds. Phil Trans R Soc B 362:489–505.

546   Fraser ON, Bugnyar T. 2010. The quality of social relationships in ravens. Anim Behav

547   79:927–933.

548   Gibbons DW. 1987. Hatching Asynchrony Reduces Parental Investment in the Jackdaw.

549   J Animal Ecol 56:403.

550   Goodwin D. 1986. Crows of the World. London: British Museum of Natural History.

551   Grodzinski U, Clayton NS. 2010. Problems faced by food-caching corvids and the

552   evolution of cognitive solutions. Phil Trans R Soc B 365:977–987.

553   Haff TM, Magrath RD. 2011. Calling at a cost: elevated nestling calling attracts

554   predators to active nests. Biol Lett 7:493–5.

555   Henderson IG, Hart, PJB. 1993. Provisioning, parental investment and reproductive

556   success in jackdaws Corvus monedula. Ornis. Scand. 24: 142–148

557   Henderson IG, Hart PJB, Burke T. 2000. Strict monogamy in a semi-colonial passerine:

558   the jackdaw *Corvus monedula*. J Avian Biol 31:177–182.

559 Insley SJ. 2001. Mother-Offspring vocal recognition in northern fur seals is mutual but

560 asymmetrical. Anim Behav 61:129–137.

561 Jolles JW, King AJ, Manica A, Thornton A. 2013. Heterogeneous structure in mixed-

562 species corvid flocks in flight. Anim Behav 85:743–750.

563 Jones IL, Falls JB, Gaston AJ. 1987. Vocal recognition between parents and young of

564 ancient murrelets, *Synthliboramphus antiquus* (Aves: *Alcidae*). Anim Behav 35:1405–

565 1415.

566 Kilner RM. 2001. A growth cost of begging in captive canary chicks. Proc Natl Acad

567 Sci USA 98:11394–8.

568 Kondo N, Izawa E-I, Watanabe S. 2010. Perceptual mechanism for vocal individual

569 recognition in jungle crows (*Corvus macrorhynchos*): contact call signature and

570 discrimination. Behav 147:1051–1072.

571 Kondo N, Izawa E-I, Watanabe S. 2012. Crows cross-modally recognize group

572 members but not non-group members. Proc R Soc B.

573 Kroodsma DE. 1989. Suggested experimental designs for song playbacks. Anim Behav

574 37:600–609.

575 Larsen O, Dabelsteen T. 1997. The "Vifa" 1 neodymium tweeter: a versatile speaker for

576 playback experiments. Bioacoustics 8:37–41.

577 Leonard ML, Fernandez N, Brown G. 1997. Parental calls and nestling behavior in tree

578 swallows. Auk 114:668–672.

579   Leonard ML, Horn AG, Mukhida A. 2005. False alarms and begging in nestling birds.

580   Anim Behav 69:701–708.

581   Lessells CM, Rowe CL, McGregor PK. 1995. Individual and sex differences in the

582   provisioning calls of European bee-eaters. Anim Behav 49:244–247.

583   Lorenz K. 1952. King Solomon's ring. London: Methuen.

584   Loretto M-C, Fraser ON, Bugnyar T. 2012. Ontogeny of social relations and coalition

585   formation in common ravens (*Corvus corax*). Int J Comp Psychol 25:180–194.

586   Madden JR, Kilner RM, Davies NB. 2005. Nestling responses to adult food and alarm

587   calls: 1. Species-specific responses in two cowbird hosts. Anim Behav 70:619–627.

588   Marzluff JM. 1988. Vocal recognition of mates by breeding pinyon jays, *Gymnorhinus*

589   *cyanocephalus*. Anim Behav 36:296–298.

590   McArthur PD. 1982. Mechanisms and development of parent-young vocal recognition

591   in the piñon jay (*Gymnorhinus cyanocephalus*). Anim Behav 30:62–74.

592   McDonald PG, Heathcote CF, Clarke MF, Wright J, Kazem AJN. 2007. Provisioning

593   calls of the cooperatively breeding bell miner *Manorina melanophrys* encode sufficient

594   information for individual discrimination. J Avian Biol 38:113–121.

595   McDonald PG, Wilson DR, Evans CS. 2009. Nestling begging increases predation risk,

596   regardless of spectral characteristics or avian mobbing. Behav Ecol 20:821–829.

597   Moreno-Rueda G. 2006. Is there empirical evidence for the cost of begging? J Ethol

598   25:215–222.

599   Proffitt FM, McLean IG. 1991. Recognition of parents' calls by chicks of the Snares

600   crested penguin. Bird Behav 9:103–113.

601   Raihani NJ, Ridley AR. 2008. Experimental evidence for teaching in wild pied

602   babblers. Anim Behav 75:3–11.

603   Rodríguez-Gironés MA, Enquist M, Lachmann M. 2001. Role of begging and sibling

604   competition in foraging strategies of nestlings. Anim Behav 61:733–745.

605   Rodríguez-Gironés MA, Zuniga JM, Redondo T. 2001. Effects of begging on growth

606   rates of nestling chicks. Behav Ecol 12:269–274.

607   Röell A. 1978. Social behaviour of the jackdaw, *Corvus monedula*, in relation to its

608   niche. Behav 64:1–124.

609   Røskaft E, Espmark Y. 1984. Sibling recognition in the rook (*Corvus frugilegus*).

610   Behav Proc 9:223–230.

611   Rowley I. 1980. Parent-offspring recognition in a cockatoo, the Galah, *Cacatua*

612   *roseicapilla*. Aust J Zool 28:445 – 456.

613   Seed AM, Clayton NS, Emery NJ. 2007. Postconflict third-party affiliation in rooks,

614   *Corvus frugilegus*. Curr Biol 17:152–158.

615   Sharp SP, Hatchwell BJ. 2005. Individuality in the contact calls of cooperatively

616   breeding long-tailed tits (*Aegithalos caudatus*). Behav 142:1559–1575.

617   Storey AE, Anderson RE, Porter JM, MacCharles AM. 1992. Absence of parent-young

618   recognition in kittiwakes: a re-examination. Behav 120:302–323.

619   Von Bayern AMP, de Kort SR, Clayton NS, Emery NJ. 2007. The role of food- and

620   object-sharing in the development of social bonds in juvenile jackdaws (*Corvus*

621   *monedula*). Behav 144:711–733.

622   Wanker R, Apcin J, Jennerjahn B, Waibel B. 1998. Discrimination of different social

623   companions in spectacled parrotlets (*Forpus conspicillatus*): evidence for individual

624   vocal recognition. Behav Ecol Sociobiol 43:197–202.

625   Wascher CAF, Szipl G, Boeckle M, Wilkinson A. 2012. You sound familiar: carrion

626   crows can differentiate between the calls of known and unknown heterospecifics. Anim

627   Cogn 15:1015–9.

628   Whiten A, Byrne RW. 1988. Tactical deception in primates. Behav Brain Sci 11:233–

629   273.

630   Wiley RH. 2006. Signal detection and animal communication. Adv Stud Behav 36:217–

631   247.

632

FIGURE LEGENDS

Figure 1. Sound spectrogram of a jackdaw feeding call (left) and a rook call (right). Produced in Syrinx (www.syrinxpc.com) with 512-point fast Fourier transform (FFT) and a Blackman window (no filter applied).

Figure 2. (A-C) Postural response intensity scores and (D-E) probability of vocal responses to the different playback treatments at three nestling ages: 10 days (A, D), 20 days (B, E) and 28 days (C, F) post-hatching. P = parents, N = neighboring jackdaws, S = stranger jackdaws, R = rooks. Means ± SE calculated from raw data are used for visual representation of postural scores. Values for vocal probability responses are derived from GLMMs in Table S3. *** indicates that among 20 and 28 day-old chicks there was a significant effect of treatment only when responses to rook calls are included in the model ($P < 0.001$; Tables S2 and S3).

Figure 3. Characteristics of nestlings' vocal responses to conspecific food calls. Panels show (A-C) latency to respond and (D-E) intensity of vocal response from principal component scores on day 10 (A, D), 20 (B, E) and 28 (C, F). P = parents, N = neighboring jackdaws, S = stranger jackdaws. Significance levels in pairwise comparisons derived by excluding factor levels from LMM analysis: $***P < 0.001$; $**$ $P < 0.01$; $* P < 0.05$. Bars show predicted means ± SE from LMMs in Tables S5 and S6.
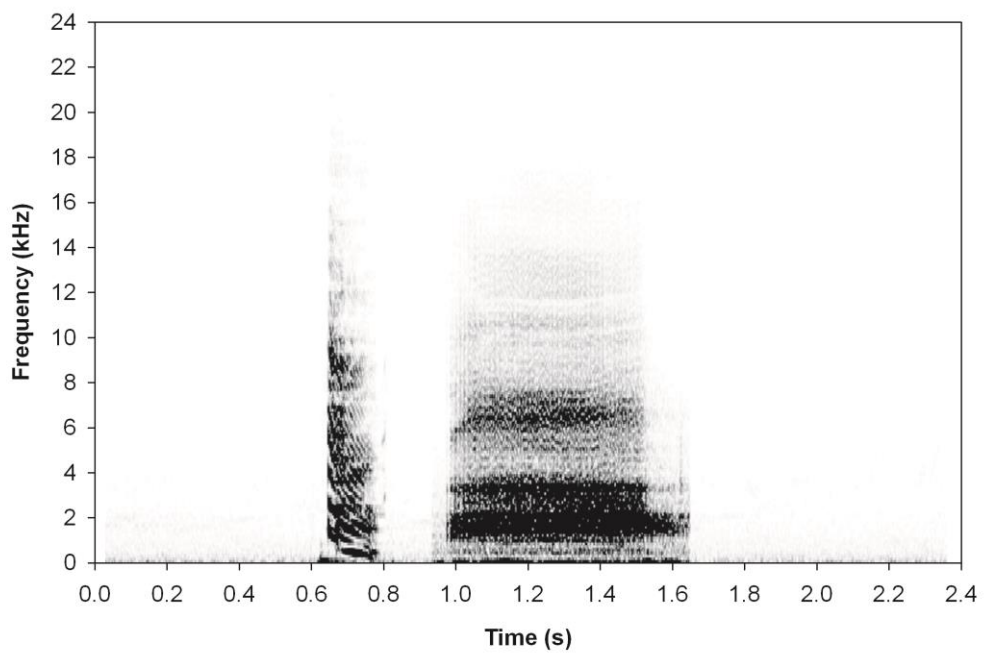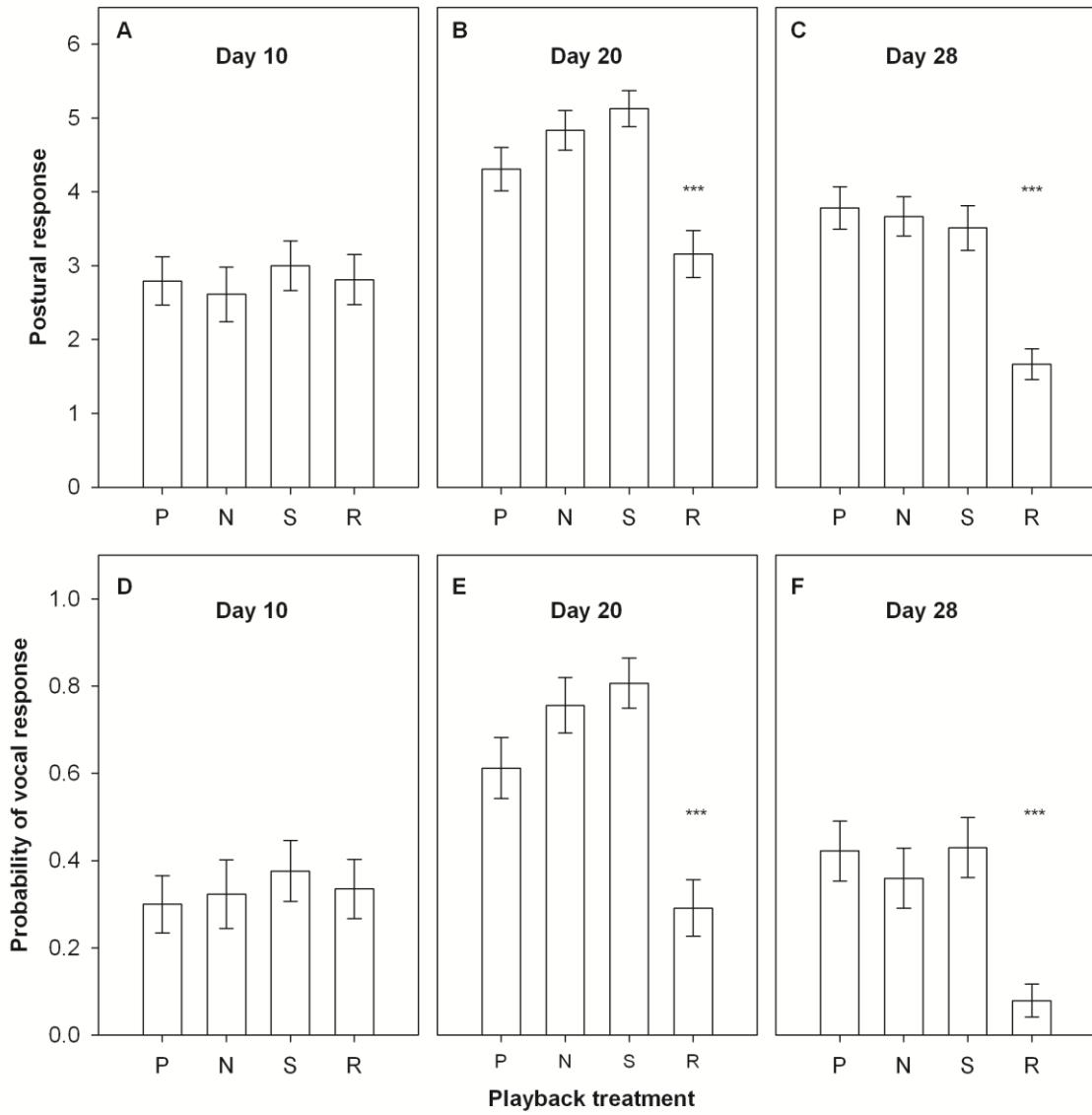
657   Figure 1

658

659

Figure 2