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Original Article

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

Lies Zandberg^{a,b}, Jolle W. Jolles^{a,c}, Neeltje J. Boogert^d and Alex Thornton^{a,e}^aDepartment of Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, UK,^bDepartment of Animal Sciences, Behavioural Ecology Group, Wageningen University, De Elst 1,Wageningen 6708WD, the Netherlands, ^cDepartment of Zoology, University of Cambridge, DowningStreet, Cambridge CB2 3EJ, UK, ^dSchool of Psychology and Neuroscience, University of St Andrews,Westburn Street, St Andrews KY16 9JP, UK, and ^eDepartment of Biosciences, Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Treliiever Road, Penryn, TR10 9FE, UK

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The ability to recognize other individuals may provide substantial benefits to young birds, allowing them to target their begging efforts appropriately, follow caregivers 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 postfledging 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 nonparental 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.

Key words: begging, Corvidae, *Corvus monedula*, food calls, parental care, social cognition, vocal recognition.

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 et al. 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 100s 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 et al. 1997; Madden et al. 2005). Food calls have been shown to be individually distinctive in a number of species (Lessells et al. 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 developed sensory and cognitive

Address correspondence to A. Thornton. E-mail: alex.thornton@exeter.ac.uk

systems, so may not yet be capable of reliable fine-scale discrimination, leading them to respond unselectively to noises near the nest (Leonard et al. 2005; Dor et al. 2006). As they become better able to discriminate, chicks may stand to benefit by begging only in response to their own parents' calls. Such selective responses may help to minimize the energetic or growth costs of begging (Kilner 2001; Rodríguez-Gironés et al. 2001; but see Moreno-Rueda 2006) and the risk attracting the attention of predators (McDonald et al. 2009; Haff and Magrath 2011) or aggressive conspecifics (Beecher et al. 1981; Proffitt and McLean 1991; Insley 2001). In species where parents continue to care for mobile young, the benefits to offspring of selective responses to parental calls may increase further as the time to leave the nest approaches. Ancient murrelets (*Synthliboramphus antiquus*), for instance, are highly precocious, and mutual parent–offspring recognition is apparent from the age of 2 days after hatching, when nestlings begin to leave their nest (Jones et al. 1987). In contrast, cavity-nesting Galah cockatoo (*Cacatua roseicapilla*) chicks do not begin responding selectively to their parents' calls until 40 days of age, 6 days before they fledge and join a crèche with fledglings from other broods (Rowley 1980).

In addition to its role in parent–offspring communication, the ability to recognize others' voices may provide important benefits in establishing and maintaining social relationships after offspring become independent (Wanker et al. 1998; Cheney and Seyfarth 2007). Among birds, corvids typically exhibit complex societies with stable individualized relationships and show behaviors in which vocal recognition has been implicated in primates (Whiten and Byrne 1988; Cheney and Seyfarth 2007), including mutual support (Seed et al. 2007; Fraser and Bugnyar 2010), alliance formation (Lorenz 1952; Emery et al. 2007; Loretto et al. 2012), and deception (Bugnyar and Kotrschal 2002; Clayton et al. 2007; Grodzinski and Clayton 2010). A handful of studies have demonstrated that corvids use individually distinctive calls to discriminate between conspecifics (pinyon jays, *Gymnorhinus cyanocephalus*, Marzluff 1988; rooks, *Corvus frugilegus*, Røskoft and Espmark 1984; jungle crows, *C. macrorhynchos*, Kondo et al. 2012; ravens, *C. corax*, Boeckle and Bugnyar 2012), but the development of this ability has received little attention. In the only test of vocal discrimination by corvid chicks, McArthur (1982) showed that pinyon jay nestlings respond more strongly to their parents' food calls than to those of other adults during the week prior to fledging, but the responses of younger chicks were not investigated. No study has yet examined when individual vocal recognition emerges during nestling development. Further research into the development of vocal recognition is thus critical for our understanding of parent–offspring communication and the emergence of later sociocognitive abilities in corvids.

We used playback experiments to investigate the development of vocal recognition in a nest box population of wild jackdaws (*C. monedula*). Jackdaws are an ideal species to examine this issue as both parents contribute extensively to offspring provisioning (Henderson and Hart 1993), announcing their feeding visits with characteristic food calls (Goodwin 1986; Cramp and Perrins 1994), and because young jackdaws may receive numerous benefits for being able to discriminate conspecific calls, both at the nestling stage and later in life. Jackdaws are cavity nesters and breed colonially, so nestlings may benefit from recognizing their parents' calls and not wasting time and energy begging in response to calls of other adults nearby. Keeping quiet unless a parental visit is certain may also avoid attracting the attention of predators and aggressive conspecifics that may attack chicks in attempts to take over the nest cavity (Röell 1978; author's unpublished data). The benefits of vocal recognition may increase further as the time for fledging approaches at around 30–35 days

after hatching. During the first 6 weeks postfledging, juveniles remain dependent on parents for food and follow them in response to food calls (Cramp and Perrins 1994). Shortly afterward, juveniles begin to form individualized relationships with nonparents and establish dominance hierarchies (Röell 1978; Henderson et al. 2000; Von Bayern et al. 2007), so the ability to recognize individuals and track their relationships could provide major benefits (Röell 1978; Emery et al. 2007). Finally, jackdaws emit regular vocalizations both while foraging and in flight, which may allow them to keep in close proximity to partners even when flying among 100s of other individuals (Jolles et al. 2013). One might therefore expect that these birds have the ability to use individual vocal recognition to identify and coordinate movements with social partners in adulthood.

We tested whether parental food calls were individually distinct and whether nestlings at different stages of development differed in their begging responses to the food calls of their own parents versus those of other adult jackdaws. To test whether nestlings would respond to any familiar adult food call, we played back food calls of parents, neighboring adults from a nearby nest box (whose calls the focal nestlings were likely 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, *C. 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 10-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- to 28-day-old nestlings would start to discriminate between calls and beg specifically in response to their own parents' calls.

MATERIALS AND 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, UK, during the 2012 breeding season (14 April to 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 8 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 around 3.5 h between 7 and 11 AM. 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). 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 posthatching), we made playback files containing 3 different calls for each of 4 treatments: 1) parents, 2) neighbor jackdaws from the same nest box site (<40 m from focal nest box; range 11–39 m), 3) stranger jackdaws from a different nest box site (>120 m from focal nest box; range 120–908 m), and 4) rooks (>100 m from focal nest box). Jackdaws show hatching asynchrony and high nestling mortality, especially among later-hatched chicks (Cramp and Perrins 1994). Mean brood size (\pm standard error [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 compensate, we added a further 4 nest boxes to the experiment to maintain a sample size of 16 nests for playbacks on day 20. One additional box was used in the experiment on day 28, giving a total of 21 nest boxes used throughout the course of the experiment (final sample sizes per age category were $N = 16$ nest boxes on days 10 and 20 and $N = 17$ on day 28). We were unable to run the “neighbor” playback treatment at some nest boxes as they did not have breeding neighbors (number of nest boxes without neighbors = 2 at day 10; 1 at days 20 and 28). To avoid pseudoreplication (Kroodsma 1989), we used different calls for each playback trial, such that the tested chicks never heard the same call more than once, and none of the calls were used more than once across the entire experiment. There were only 5 exceptions where we did not record sufficient numbers of parental food calls, forcing us to use the same call as a playback stimulus twice, but we played this call at different focal nest boxes. As every call recording contained some ambient noise, we inserted the calls into a playback file with similar ambient noise extracted from our recordings. The ambient noise was faded in for 20 s at the start of the playback file and faded out for 20 s at the end, with 30 s of ambient noise in between the 3 calls, so each playback treatment lasted 100 s in total.

We played the playback files in an uncondensed WAV format to chicks in the nest box from an iPod Mini connected to a high-fidelity Vifa D26 NC-05-06 neodymium tweeter speaker (commonly used in avian playback experiments; see Larsen and Dabelsteen 1997) and a Kemo 12v amplifier. The speaker was attached to a pole of length 4 m and held in front of the nest box out of the line of sight of the nestlings. Playback amplitude was calibrated prior to the experiment by recording calls played from the speaker in 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 (0.5 m) were standardized across all playback trials. To reduce the potential for habituation to playbacks, there was a break of 15 min 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 h. 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 8 known individuals, obtaining 8 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) with the batch spectrogram correlation function in Raven Pro 1.4 acoustic analysis software (Cornell Lab Of Ornithology, Ithaca, NY). Rather than restricting comparisons to a predetermined and potentially incomplete set of variables, SPCC analysis compares all the measurable spectral features of 2 calls over time by “sliding” them past each other and obtaining the peak correlation score, generating a matrix of correlation coefficients between 0 and 1 for all possible pairwise comparisons (Clark et al. 1987). To test the hypothesis that the correlation value within individuals is greater than the correlation between individuals, we used a procedure based on the Mantel test. We compared the SPCC matrix to a second “hypothesis matrix” containing a binary code, with “1”s representing within-individual comparisons and “0”s representing between-individual comparisons in the equivalent positions. A significant positive correlation between the SPCC correlation matrix and the hypothetical matrix indicates that the within-individual correlation values are higher than the between-individual values (Sharp and Hatchwell 2005). To check whether subtle similarities in background noise within nest boxes could be responsible for apparent within-individual similarity in calls, we also ran a similar analysis based on SPCC comparisons of the 1s of background noise preceding all calls.

Nestling responses

To make maximal use of the data, we analyzed all possible responses to every playback call (4 treatments, with 3 calls per treatment, giving a maximum of 12 potential chick responses per nest box for each age category) using multifactorial analyses. We used generalized estimating equations (GEE) for ordinal response terms and linear mixed models (LMMs) or generalized LMMs (GLMMs) for normal or nonnormal data, respectively. Nest box identity was fitted as a random factor to control for repeated measures in all models. Chick age (10, 20, or 28 days) and playback treatment (parent, neighbor, stranger, or rook), were fitted as explanatory terms, along with call order (first, second, or third call in each playback treatment) and the number of chicks in the nest. As disturbance at the nest may have deterred parents from visiting during the experiment, leading to changes in chicks’ hunger levels and begging responses, treatment order (first, second, third, or fourth playback treatment) was fitted as an additional explanatory term. We initially included all explanatory terms in the models. All possible 2-way interactions between them were investigated and terms were sequentially dropped until the minimal model contained only significant terms remained in the model. Probability values for significant terms were derived from this minimal model, whereas values for nonsignificant terms were obtained by adding each term individually to the minimal model (Crawley 2002). Model

residuals were visually inspected to ensure homogeneity of variance, normality of error, and linearity. Post hoc analyses of differences between levels of interest within categorical variables were conducted by sequentially excluding levels from models to enable comparisons of the remaining category levels. Wald statistics (χ^2) for models with nonnormal response terms are quoted with numerator degrees of freedom for each explanatory term; for LMM with normal response terms we quote F statistics with numerator and denominator degrees of freedom, separated by a comma. Means are quoted \pm SE throughout. Tables of results for all multifactorial analyses including all effect sizes and SEs are provided in the [Supplementary Material](#). The total sample size for full analyses was $N = 21$ nest boxes across all age categories (for analyses within age categories, $N = 16$ on days 10 and 28; $N = 17$ on day 28). All analyses were conducted in Genstat 16.1 (VSN International) except where otherwise specified.

Nestling postural responses

From the nest box videos, we scored the intensity of the maximum postural responses seen among the nestlings to each playback call, from 1 (no response at all) to 6 (full begging response: body and neck fully extended, with open gape; see [Supplementary Table S1](#)). A response score of 0 was included for cases where the chick quickly cowered down (typically in the far corner of the nest box) in response to the call. Fifteen percentage of videos were analyzed by a second coder blind to experimental treatments (interobserver reliability: kappa = 0.87; $P < 0.001$). Postural responses were analyzed using a GEE with ordinal logistic method and an exchangeable correlation structure in SPSS (version 20; IBM Corp). Nest box was fitted as the subject variable to control for repeated measures.

Probability of vocal response

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

Characteristics of vocal response

Subtle differences in vocal response features may provide evidence for vocal discrimination that is not apparent by examining vocal response probability or postural responses alone (Boeckle and Bugnyar 2012). We therefore used LMMs to analyze chicks' latency to respond to broadcast calls and the total duration of chick begging, focusing specifically on responses to conspecific food calls. We also used the Choose Measurements tool in Raven Pro 1.4 to extract from the spectrograms (measured with window length: 2.67 ms; frequency resolution: 188 Hz) a number of acoustic parameters that reflect the intensity of vocal responses: peak amplitude (dimensionless sample units, u), root mean square or "effective" amplitude (u), total energy (dB), peak frequency (Hz), peak power (dB), and average power (dB) of the first call. As these parameters show substantial autocorrelation, we used principal components analyses (PCA) with a varimax rotation to obtain composite measures of vocal begging intensity, using a minimum eigenvalue of 1.0 to determine the number of components extracted from the PCA. We then used the rotated scores from each component as response variables in LMM analyses with nest box as a random term to control for repeated measures. Initial analyses showed that variables loaded differently on principal components at different ages, so we conducted separate analyses on PCA scores for playbacks at days 10, 20, and 28. As it was not possible to determine which nestling in a brood was calling, total brood responses were used as the units of analysis.

RESULTS

Distinctiveness of adult food calls

Jackdaws produce food calls of short duration (range: 88–179 ms) with a peak frequency between 937.5 and 5438 Hz ($N = 64$; [Figure 1](#)). Rook calls are acoustically different from jackdaw calls, with a longer duration of 390–814 ms and peak frequency of 1378–2067 Hz ($N = 24$; [Figure 1](#)). SPCC analyses of jackdaw call structure showed that calls from the same individual were more similar in acoustic structure than calls from different individuals (mean correlation coefficient within individuals = 0.53 ± 0.01 ; between

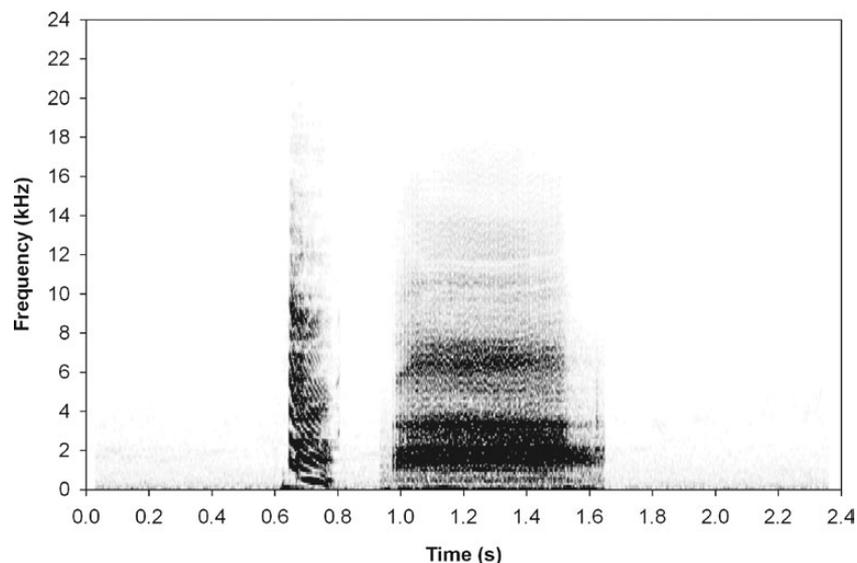


Figure 1

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).

individuals = 0.35 ± 0.003). A Mantel test confirmed that within- and between-individual correlation coefficients were significantly different (10 000 permutations, $r = 0.35$, $P < 0.005$), indicating that jackdaw food calls are individually distinctive. Within-individual call similarity could not be an artifact of background noise, as a Mantel test revealed no significant difference in SPCC values of background noise from recordings within and between individuals (10 000 permutations, $r = 0.05$, $P = 0.11$).

Nestling postural responses

There was a significant interaction between age and playback treatment, with nestlings of 10 days of age responding equally to all treatments, whereas older nestlings showed significantly reduced responses to rook calls compared with conspecific calls (Figure 2A–C; GEE; age \times treatment: $\chi^2_6 = 16.56$; $P < 0.011$; Supplementary Table S2). Restricting the analysis to 10-day-old nestlings confirmed there was no effect of treatment at this age (GEE: $\chi^2_3 = 0.125$; $P = 0.989$). GEE analysis restricted to older nestlings showed a

significant effect of treatment, with lower responses to rook than jackdaw calls (GEE: $\chi^2_3 = 22.95$; $P < 0.001$). Excluding responses to rooks from this analysis, nestlings responded with similar intensity to all jackdaw treatments (GEE: $\chi^2_2 = 0.49$, $P = 0.783$).

Probability of vocal response

GLMM analysis of whether or not nestlings begged in response to calls revealed a significant interaction between nestling age and playback treatment (Figure 2D,E; GLMM: $\chi^2_6 = 24.74$; $P < 0.001$; Supplementary Table S3), controlling for the effect of treatment order ($\chi^2_3 = 11.88$; $P < 0.008$). Restricting the GLMM analysis to 10-day-old nestlings showed no significant difference in response to any of the different treatments ($\chi^2_3 = 1.20$; $P = 0.753$). On days 20 and 28 there was a significant effect of treatment, with nestlings being less likely to respond to rooks than to conspecific calls (GLMM on 20- and 28-day-old nestlings; effect of treatment: $\chi^2_3 = 40.44$; $P < 0.001$). However, they did not respond significantly differently to the 3 categories of jackdaw calls: excluding

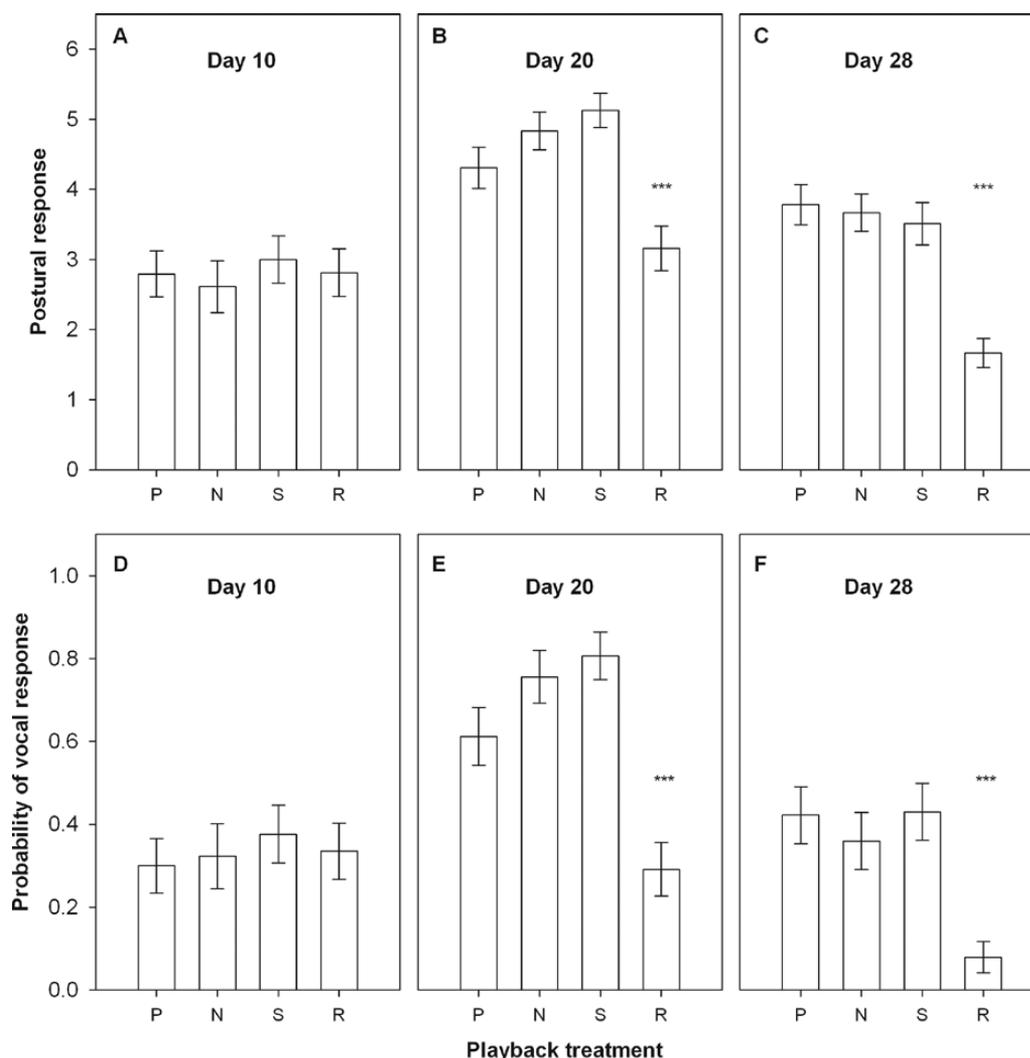


Figure 2

(A–C) Postural response intensity scores and (D and E) probability of vocal responses to the different playback treatments at 3 nestling ages: 10 days (A and D), 20 days (B and E), and 28 days (C and F) posthatching. P = parents, N = neighboring jackdaws, S = stranger jackdaws, R = rooks. Means \pm SE calculated from raw data are used for visual representation of postural scores. Values for vocal probability responses are derived from GLMMs in Supplementary 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 ($P < 0.001$; Supplementary Tables S2 and S3).

responses to rooks from GLMM there was no significant difference in responses to jackdaw call treatments ($\chi^2_2 = 3.26$, $P = 0.196$).

Characteristics of vocal responses

In cases when nestlings responded vocally to jackdaw food calls (i.e., excluding cases with no vocal response), the duration of begging calls declined as chicks grew older (LMM: $F_{2,201} = 20.05$; $P < 0.001$; Supplementary Table S4), but was unaffected by playback treatment (treatment; $F_{2,195} = 0.54$; $P = 0.582$; treatment \times age: $F_{4,188} = 4.55$; $P = 0.287$). In contrast, analysis of nestlings' latency to beg revealed a significant interaction between age and treatment (Figure 3A–C; LMM: age \times latency $F_{4,188} = 2.42$; $P = 0.050$; Supplementary Table S5; response variable normalized for analyses with a Box–Cox transformation). LMM analyses within age groups showed no significant differences between treatments at age 10 ($F_{2,38} = 0.67$; $P = 0.519$) but at age 20 there was a significant effect of treatment ($F_{2,89} = 4.77$; $P = 0.011$). Sequentially excluding treatment levels from the LMM revealed that chicks were

significantly faster to respond to parents than to both neighbors ($F_{1,51} = 8.75$; $P = 0.005$) and strangers ($F_{1,52} = 4.45$, $P = 0.044$). At day 28 there was a marginally nonsignificant effect of treatment (LMM; $F_{2,50} = 3.10$; $P = 0.054$) with faster responses to parents and neighbors than to strangers.

All PCAs on acoustic parameters yielded 2 principal components, with PC1 explaining 61–77% and PC2 16–21% of the variance in the data across the 3 age categories. Scores from these components were unrelated to playback treatment on day 10 (LMMs; PC1: $F_{2,38} = 0.13$; $P = 0.879$; PC2: $F_{2,38} = 0.83$; $P = 0.444$) or 20 (PC1: $F_{2,83} = 0.16$; $P = 0.857$; PC2: $F_{2,83} = 1.08$; $P = 0.344$). For begging calls produced on day 28, however, PC1 scores differed significantly between treatments, (Figure 3D,E; LMM: $F_{2,52} = 14.68$; $P < 0.001$; Supplementary Table S6). At this age, peak amplitude, peak power, and energy all had high loadings on PC1 (see Supplementary Table S7 for rotated loadings of variables on each extracted component). Sequentially removing treatment levels from the LMM analysis revealed that PC1 scores were significantly higher in response

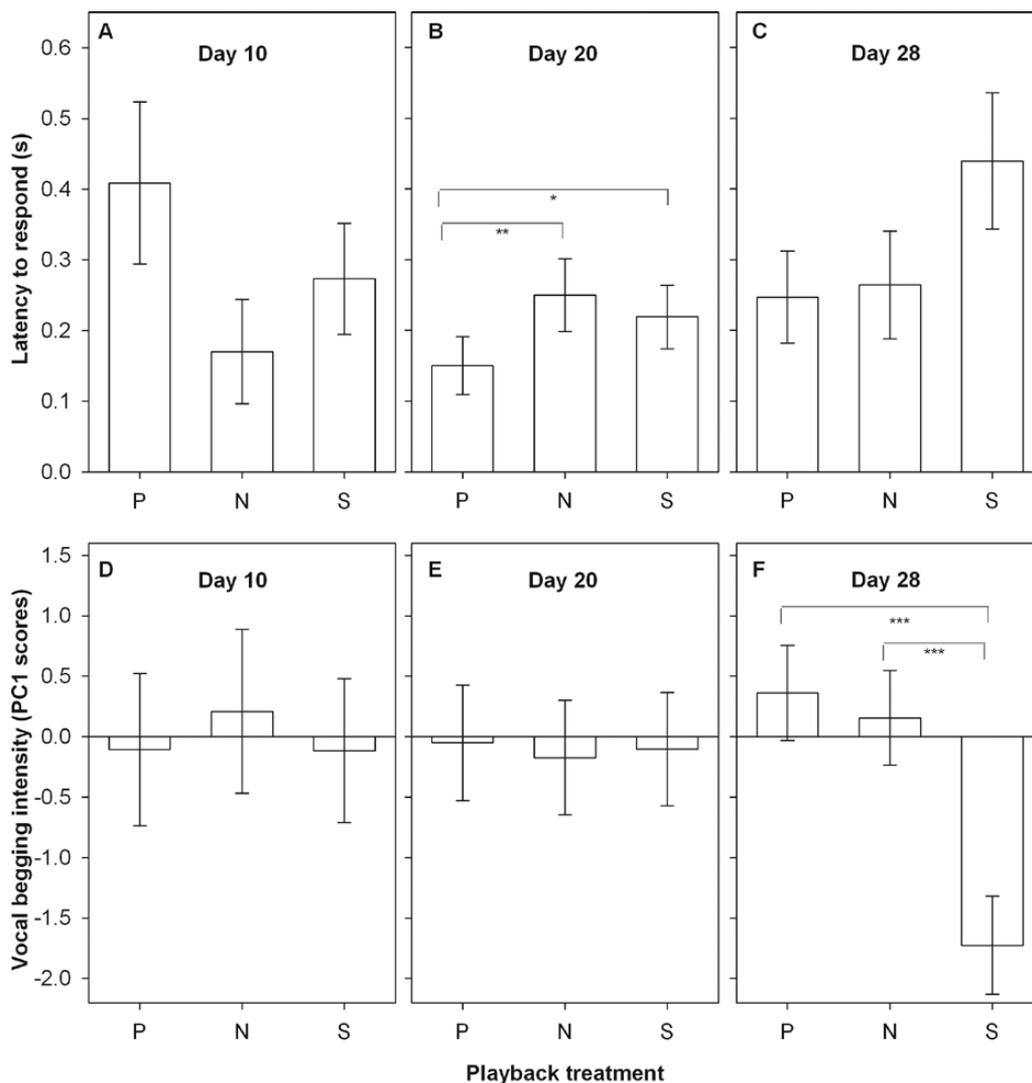


Figure 3

Characteristics of nestlings' vocal responses to conspecific food calls. Panels show (A–C) latency to respond and (D and E) intensity of vocal response from principal component scores on day 10 (A and D), 20 (B and E), and 28 (C and 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 \pm SE from LMMs in Supplementary Tables S5 and S6.

to parents and neighbors than to strangers (parents vs. strangers: $F_{1,39} = 20.96$; $P < 0.001$; neighbors vs. strangers: $F_{1,30} = 12.55$; $P < 0.001$) but responses to parents and neighbors did not differ ($F_{1,32} = 0.09$; $P = 0.765$). PC2 scores did not differ between treatments ($F_{2,53} = 0.82$; $P = 0.449$).

DISCUSSION

In this study we showed that the food calls of jackdaws, like jackdaw contact calls (Wascher et al. 2012) and the calls of several other corvid species (Marzluff 1988; Kondo et al. 2010; Boeckle et al. 2012) are individually 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 posthatching. 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 et al. 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 and 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 2 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. Although 10-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 jackdaw nestlings may in fact be capable of distinguishing between conspecific calls prior to fledging. Faster responses to parents than to neighbors on day 20 provide some indication that nestlings may perceive differences in these calls, both of which are likely to be familiar and heard on a daily basis. However, other results show differences only between strangers and the 2 familiar call categories. We therefore tentatively suggest that jackdaw chicks can at least discriminate between familiar and unfamiliar calls.

Together our results suggest that while jackdaws may develop the perceptual and cognitive resources to distinguish between conspecific calls while in the nest, they may derive few benefits from selectively limiting their begging responses by discriminating between the calls of parents and other adults. The principal costs of indiscriminate begging are likely to be the time and energy costs of unrewarded begging displays and the risks of attracting predators or aggressive conspecifics (Kilner 2001; Haff and Magrath 2011). However, jackdaw nestlings may substantially reduce many of these costs by ceasing to beg to non-jackdaw noises in the environment without needing to discriminate further between conspecific calls. Moreover, as chicks grew older, their greater size and ability to sit upright, which was evident from nest box video recordings, may have enabled them to look through the cavity entrance to see parents arriving with food. Consequently, nestlings in the final days before fledging may have been less reliant than younger chicks on food calls to stimulate begging, which could help explain the overall reduction in responsiveness to food calls from day 20–28. Finally, although we and others have recorded instances of nest predation and intraspecific attacks, these events appear to be rather rare (Röell 1978; Gibbons 1987). At our study site, we have observed a single (nonlethal) conspecific attack on a nestling. Most suspected instances of nest predation at our study site occurred when entire broods disappeared overnight, suggesting that the culprits may have been nocturnal predators, rather than diurnal predators that might be attracted by chick begging (author's unpublished data). Thus, for jackdaw nestlings the costs of begging may be insufficient to warrant highly selective responses to parents. Our results contrast with findings from other species living in similar conditions, in which nestlings do show vocal recognition of their parents' calls. For example, galah cockatoos, like jackdaws, are cavity nesters and nestlings have been shown to respond preferentially to their parents' calls a week or so before fledging (Rowley 1980). Similar results were found for nestling pinyon jays, a gregarious corvid species (McArthur 1982). Both pinyon jays and galah cockatoos live in fission–fusion societies similar to those of jackdaws, but differences in discrimination by nestlings may be explained by differences in the relative costs of individual begging, for instance, if jackdaw nestlings are under relatively lower risk of predation.

Previous studies of offspring–parent vocal recognition in birds have tended to rely on gross response measures such as the presence or absence of a response or categorical measures of chick posture and

movements toward speakers (Beer 1971; Rowley 1980; McArthur 1982; Storey et al. 1992; Aubin and Jouventin 1998). Our work indicates that detailed examination of vocal response characteristics may reveal discriminatory abilities that would not otherwise be apparent. In jackdaws, subtle differences in the latency and vocal intensity of nestling responses may reflect the early emergence of a skill that is likely to be critical later in life when fledglings must follow their parents and form social relationships. Postfledging experiments, such as a preference test in which fledglings are presented with calls from 2 different individuals simultaneously, may shed more light on the development of individual recognition in this species. Comparative experiments between species may allow us to elucidate the causes of variation in the development of vocal recognition. Furthermore, despite several reports of individual vocal recognition in captive corvids (Røskaft and Espmark 1984; Boeckle and Bugnyar 2012; Kondo et al. 2012), little is known about how corvids employ vocal recognition in their natural environments (but see Marzluff 1988). Studies of vocal recognition in the wild will provide further insights into the mechanisms underlying the sophisticated sociocognitive skills for which corvids are well known (Emery and Clayton 2004).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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