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Who’s calling? Vocal individuality in carrion and hooded crow nestlings and fledglings.

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Contents

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Authors: Hannah Gidl*, Sara Binder*, Anna N Osiecka** and Barbara C Klump**

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Zusammenfassung

Akustische Kommunikation spielt in einer Reihe von Interaktionen im Tierreich eine Rolle. Vokalisationen können Informationen zur Identität eines Individuums enthalten. Diese Signale richtig zuzuordnen kann besonders in Interaktionen zwischen Verwandten relevant sein, insbesondere bei in Kolonien brütenden Arten, um fehlgeleitete elterliche Fürsorge zu vermeiden. Eltern mancher Vogelarten können außerdem zwischen einzelnen Individuen ihres Nachwuchses unterscheiden. Um an Vokalisationen erkannt werden zu können, müssen diese zureichend individuelle akustische Eigenschaften aufweisen. Diese stimmliche Individualität wurde bei verschieden Vogelarten bereits im Nestlingsstadium nachgewiesen und kann sich in ihrer Ausprägung über die Entwicklung hinweg verändern, abhängig von ihrem adaptiven Wert. Weiters kann sich ihre Ausprägung zwischen verschiedenen Ruftypen und affektiven Zuständen unterscheiden. Um die diesen Unterschieden zugrundeliegenden Faktoren aufzuschlüsseln, werden mehr Studien von Arten mit verschiedenen 'life histories' und Sozialstrukturen benötigt. Diese Masterarbeit untersucht die Entwicklung stimmlicher Individualität bei Raben- und Nebelkrähen (*Corvus corone* und *Corvus cornix*) im Nestlingstadium sowie in den ersten zwei Wochen nach dem Flüggewerden. Ihre Rufe konnten über verschiedene Perioden und Kontexte hinweg dem korrekten Individuum zugeordnet werden. Das Ausmaß an Information zur Identität des rufenden Individuums scheint sich darüber hinaus zwischen verschiedenen Zeitabschnitten und Kontexten zu unterscheiden. Die Individualität wird von mehreren akustischen Parametern codiert, die sich über verschiedene akustische Domänen erstrecken. Weitere Studien sind notwendig, um zu untersuchen wie Eltern und Geschwister diese Information verwenden.

Abstract

Acoustic communication plays a role in numerous animal interactions. Vocalisations can carry information on individual identity. Recognition of these cues is of special importance in family interactions, especially in order to avoid misdirected parental care in colonial species. Bird parents have also been found to be able to discriminate between individual nestlings. Sufficiently distinct acoustic features are needed in order to be recognisable by voice. Such vocal individuality has been found to be present as early as the nestling stage for multiple species and may vary in its degree over development depending on its adaptive value. It can also differ depending on call type and affective state. More studies on species with different life histories and social structures are needed to disentangle the factors underlying these differences. The study at hand investigates the development of vocal individuality in carrion and hooded crows (*Corvus corone* and *Corvus cornix*) in the nestling and fledgling stage. I found that their calls can be assigned to the individual above chance level across contexts and periods. The degree of individuality coding may differ between periods as well as between contexts. This individuality was found to be coded through a variety of parameters spanning different domains of sound. Further studies are needed to investigate how parents and siblings might use this information.

1. Introduction

Acoustic communication plays an important role in numerous animal interactions. In birds, vocal signals are a prominent and extensively studied aspect of communication (Catchpole et al., 2008).

The ontogeny of their vocalisations, in particular birdsong, has received special attention, and birds are considered one of the most important models for studying vocal learning. Traditionally, bird species are regarded as either vocal non-learners or vocal learners, with three groups being part of the latter category: Hummingbirds, parrots and songbirds (Loo and Cain, 2021). Vocal non-learners are able to develop normal adult vocalisations without needing specific auditory input (e.g. doves, Lade and Thorpe, 1964), while vocal learners require hearing conspecifics as an auditory model during development (Kroodsma et al., 1982). Studies on the vocal development of songbirds have focused mostly on song rather than calls, a bias that could limit our understanding of the spectrum of vocal learning abilities and the diversity of vocal development (Loo and Cain, 2021). Previous studies on vocal learners have shown that nestling vocalisations such as begging calls may gradually transition into adult calls, thereby serving as the basis of the adult repertoire (e.g. in spanish sparrows, *Passer hispaniolensis*, Marques et al., 2011 and kea parrots, *Nestor notabilis*, Wein et al., 2021). In Magpies (*Pica pica*), this was found to apply only to some call types, while others seemed to appear without any transitional forms (Redondo, 1991). The development toward adult calls is dependent not only on learning, but also on the morphological changes that birds undergo during ontogeny, which are especially rapid in altricial birds (Ricklefs, 1983). Calls changing towards more adult-like vocalisations may therefore depend on the physical constraints on certain acoustic parameters. In spanish sparrows for example, the call duration of nestling calls increases with age, likely made possible by a larger capacity to exhale a continuous flow of air caused by an increase in body size (Marques et al., 2011). However, the dura-

tion of begging calls also serves as a signal for need/hunger (see e.g. Leonard and Horn, 2001; Marques et al., 2008; Reers and Jacot, 2011) thereby needing to be changed flexibly within a given developmental stage. Apart from signaling need through changes in call duration and frequency parameters, begging calls can also serve as a signal of identity to a nestling's parents (e.g. Reers and Jacot, 2011; Levréro et al., 2009).

Such recognition of specific individuals based on the acoustic features of their vocalisations (i.e. individual vocal recognition) is relevant not only between parents and their offspring but also in numerous other types of interactions, having evolved multiple times and being found in birds as well as in mammals and amphibians (for a review, see Carlson et al., 2020). Recognition through acoustic cues can take place even when visual cues to identity are obscured by obstacles or darkness (Shapiro, 2010) as well as over long distances (see e.g. McComb et al., 2003), making this type of recognition superior to olfactory and visual recognition in some contexts.

An animal may be able to recognize one single individual from all others (e.g. their mate from an array of strangers: laughing gulls, *Leucophaeus atricilla*, Beer, 1971; as cited in Carlson et al., 2020) but there are also numerous cases of recognition of multiple individuals from one another (e.g. in common starlings, *Sturnus vulgaris*, Gentner and Hulse, 1998).

For the receiver, recognizing an individual can help determine the risk or benefit of a possible interaction with the vocalising individual (based on whether they are a competitor, a partner, a parent, etc.) (Tibbetts and Dale, 2007; Wiley, 2013). Furthermore, the receiver may be able to evaluate other information provided by the vocalisation based on the identity of the caller (e.g. the reliability of alarm calls, Western Australian magpies, *Gymnorhina tibicen*, Silvestri et al., 2019). For the signaler, being recognized is adaptive when it leads to increased cooperation from related individuals (e.g. Medvin and Beecher, 1986) or strengthens reciprocal relationships (e.g. Schel et al., 2013). Another positive fitness outcome can be a reduction in aggression from a competitor in dominance (e.g. Tibbetts, 2004) or territorial interactions ('dear enemy effect', Temeles, 1994).

Recognizing individuals is therefore of special relevance in species that are highly social or whose societies are based on strong dominance hierarchies (Carlson et al., 2020), as well as when interactions with the same individuals occur repeatedly over long time periods (Dreiss et al., 2014). For example, female great tits (*Parus major*) can identify their

partners' songs (Lind et al., 1996) and song sparrows (*Melospiza melodia*) can acoustically discriminate between neighbours and strangers as well as between individual neighbours (Stoddard et al., 1991). Vocal recognition can also be important in family interactions: For example, siblings have been shown to recognize each other (spectacled parrotlets, *Forpus conspicillatus*, Wanker et al., 1998) and may even adjust their competitive efforts according to relatedness with nestmates through acoustic kin recognition (barn swallows, *Hirundo rustica*, Boncoraglio et al., 2009) or use individual vocal recognition to determine siblings' motivation to compete for food brought to the nest by parents (barn owls, *Tyto alba*, Dreiss et al., 2014). Parent-offspring recognition is of special significance in colonially breeding species, where parents have to avoid misdirecting their care toward unrelated offspring (e.g. Levréro et al., 2009). Parents can also discriminate between individual offspring, as has been found in black redstarts (*Phoenicurus ochruros*), where parents preferentially feed specific nestlings (Draganoiu et al., 2006).

In order for animals to discriminate between calls from different individuals, sufficiently distinct acoustic features need to be present in their vocalizations. Unique features likely exist in most vocalizing species due to slight morphological differences in each individuals' vocal tract (Carlson et al., 2020). However, vocal individuality can also be affected by the social environment of an animal: Individuals may adjust the acoustic structure of their vocalisations to become more similar to social partners whose calls they hear frequently. African penguins (*Spheniscus demersus*) for example seem to match their vocalisations to those of members of their colony (Baciadonna et al., 2022) and little auks (*Alle alle*) show a tendency to match the structure of their calls to their partners' (Osiecka et al., 2023). In common ravens (*Corvus corax*), pairs seem to match their long-distance calls to become vocally similar (Luef et al., 2017).

Family signatures can be learned as early as during the embryonic stage, mitigating the risk of misdirected parental care toward brood parasites (Colombelli-Négrel et al., 2012).

The degree of inter-individual discriminability of calls may also change throughout ontogeny, likely depending on the adaptive value of being recognisable. In red-crowned cranes (*Grus japonensis*) for example, the discriminability of the calls of the chicks increases from a first phase, in which the parents are territorial, to a second phase, in which the family transitions to flock living, a lifestyle change that leads to an increased risk of

confusing the parents' own chicks with those of conspecifics (Klenova et al., 2009). However, to really disentangle what influences such ontological changes in vocal individuality, further studies on animals from different groups and different life histories are needed.

The individuality of calls can also be influenced by the affective state of the emitter. For example, the distress calls of little auk (*Alle alle*) chicks have been found to have a lower potential for individuality coding than their begging calls (Osiecka et al., 2024b). In the same vein, the degree of individual distinctiveness of calls has been found to differ between call types in some species, suggesting different selection pressures underlying the evolution of vocal individuality for different contexts (Linn et al., 2021). Three hypotheses, which are not necessarily mutually exclusive, have addressed this difference. First, the "distance communication hypothesis" (Mitani et al., 1996) suggests that call types used over long distances without visual contact should be more individually distinct to compensate for the lack of other modes of identification. Second, the "social function hypothesis" (Snowdon et al., 1997) predicts that calls directed towards specific individuals in intragroup social interactions (e.g. contact calls) should be more individualised than calls directed to all members of the group (e.g. alarm calls). This hypothesis was later extended (Lemasson and Hausberger, 2011) to suggest that vocal individuality should be highest in call types used in affiliative contexts, intermediate in call types associated with aggressive interactions and lowest in calls directed towards all group members or related to general activities. Lastly, the "acoustic structure hypothesis" involves the production mechanism of different call types and the resulting acoustic structure of calls (see e.g. Leliveld et al., 2011). In this regard, it has been suggested that narrow-band harmonic calls are better suited to convey information about an individual's identity (e.g. Yin and McCowan, 2004).

Corvids represent an interesting model for studying aspects of communication, including acoustic communication (Suzuki and Izawa, 2023; for a review see Wascher and Reynolds, 2025), as they live in complex social societies with dominance hierarchies and long-term affiliative relationships and show highly complex cognitive skills (e.g. Bugnyar, 2024; Taylor, 2014). Carrion crows (*Corvus corone*) and hooded crows (*Corvus cornix*) are currently considered two distinct species (Glandt, 2012). They are, however, regarded as being part of the same palearctic superspecies (Bauer et al., 2005), with two stable hybrid zones, one of which runs through central Europe (De Knijff, 2014). Both are among

the corvid species that are frequently used in social cognition research (e.g. Hillemann et al., 2014; Wascher, 2015). Carrion crows are known to have a complex and, at times, cooperative social life, with their breeding tactics ranging from territorial pair breeding to, in some cases, cooperative breeding (Baglione et al., 2002) and may therefore have both the ability and need for a complex system of vocal communication (Siriwardena, 1995). Breeding pairs are monogamous and usually territorial. The nestling period lasts around 30 days, but the offspring stay with their parents after fledging and are fed for around five more weeks. After four to eight weeks, the young will usually leave the parental territory and join flocks of non-breeders (Bezzel, 1993).

The social complexity of crows' societies might lend relevance to individual vocal signatures and their recognition. Indeed, jungle crows utilise so called "contact calls" for individual recognition of conspecifics (Kondo et al., 2010) and a previous study has shown that carrion crows are likely able to discriminate between alert calls from reliable and unreliable conspecifics (Wascher et al., 2015). There has been a study on the vocal repertoire of carrion crows almost 30 years ago (Siriwardena, 1995), but to my knowledge, practically nothing is known about their vocal ontogeny, nor about when individual vocal signatures develop and how they may change throughout the development of nestlings and fledglings. Subsequently, there have not been any studies on how the individuality of calls may differ depending on context at these life stages of carrion and hooded crows.

For the Master thesis at hand, we recorded calls from five carrion and hooded crows over a month-long period to investigate how their vocal individuality develops from 11-14 days old up to until two weeks after fledging. The resulting data provided us with the opportunity to be the first to address a number of questions regarding the ontogeny of vocal individuality in these birds. Namely, to shed light on 1) whether their vocalisations are already individually distinct during these life stages and can thereby be assigned to the individual based on acoustic parameters across the recorded month; 2) whether this vocal individuality varies between different periods of the recorded month; 3) whether the vocal individuality varies between calls recorded in different behavioural contexts, and 4) which acoustic parameters this individuality is coded in. Additionally I wanted to investigate 5) how call duration, an acoustic parameter commonly found to be important in both hunger signaling as well as vocal individuality, changes throughout ontogeny and whether this change differs between individuals. And lastly, I set out to 6) document whether there

are individual differences in calling behaviour (i.e., how frequently an individual emitted calls in different behavioural contexts).

Regarding the first question, I predicted that 1) calls could be assigned above chance level to the individual and that chicks would already be vocally individualized during the earliest week we recorded, since previous studies have found vocal individuality to be present from early on in numerous bird species (e.g. Levréro et al., 2009; Cornec et al., 2022; Osiecka et al., 2024b). For the second question, I hypothesized that 2) the individuality of calls would increase over the recorded month. This was predicted to be the case because the transition from nestlings to fledglings represents a shift to a lifestyle with an increasing risk of the offspring intermingling with the chicks of other pairs. The adaptive value of being recognizable by voice would thereby increase. Furthermore, as the offspring prepares to leave the parents and join non-breeder flocks, it may benefit from stronger vocal individuality, as such a group represents a socially more complex environment. Concerning a possible difference in vocal individuality between calls from different behavioural contexts (hereafter referred to as "contexts"), I predicted that, in line with the social function hypothesis (as expanded by Lemasson and Hausberger, 2011), 3) begging calls would be more individually distinct than calls from other contexts, as they are directed specifically at the parents. However, it was not possible to make clear predictions about other contexts, as to my knowledge, no previous studies documenting the kinds of contexts in which crow chicks might vocalise exist. Generally, however, I expected calls from affiliative contexts to be more individualised than those from aversive contexts or situations with neutral fitness outcomes / related to general activities. For the parameters coding individuality, I predicted that 4) individuality would be coded by a combination of parameters, likely spanning both the temporal and the frequency domain, as this has been found to be the case in previous studies of vocal individuality in birds (see e.g. Reers and Jacot, 2011; Levréro et al., 2009; Osiecka et al., 2024a). For a change in begging call duration with age, I hypothesized that 5) call duration would increase with age, reflecting the physical development and subsequent capacity for exhaling a longer continuous flow of air, and possibly also a change towards more adult-like vocalisations. As individuals may develop at different speeds due to factors such as a chick's overall health, I expected an individual difference in how quickly this change would occur.

2. Material and Methods

2.1 Study site and population

From March until May 2024, we monitored wild nests of pairs of hooded and carrion crows (*Corvus cornix* and *Corvus corone*) in the districts of Bad Vöslau, Gänserndorf and Hohenau in lower Austria (once a week in the first two weeks of March and two to three times per week from then onward until 10-14 days after hatching of the observed chicks).

On May 1st 2024, five crow nestlings (three females and two males) were acquired from two wild nests (Ethics permit: Approved by the Animal Ethics and Experimentation Board at the Faculty of Life Sciences, University of Vienna, application no. 2023-033; birds obtained under permissions issued by the Bezirkshauptmannschaft Baden, BNL2-J-082/116, and Gänserndorf, GFL-J-0712/002) at an estimated age of 10-14 days. Because the crows originate from a hybridization zone between the two species, we did not differentiate between species. The nestlings were then hand-raised at Haidlhof Research Station near Bad Vöslau, Austria following established procedures (see below) until fledging at 25-29 days of age. They were individually marked (initially by colouring their nails and after fledging by leg rings).

During the hand-raising period, the nestlings were housed indoors in two artificial nests. The nest properties were manipulated for a different experiment. One nest's inside was lined with paper and contained two genetic siblings. Another nest contained natural materials, such as sticks, straw and feathers, and consisted of two related siblings as well as one unrelated social sibling from the other wild nest (Tab. 8, supplementary material). Three other crows that were not part of this study were hand-raised in one additional nest in the same room. The birds were subjected to natural daylight hours through two windows. The windows were kept open for most of the day, enabling the chicks to hear wild and captive adult crows. They were hand-fed every two hours from 6 a.m. to 10 p.m.

with a diet containing a mixture of ground fruit muesli, day-old chicks, mealworms, fruit, vegetables, feed lime, Korvimin, and fennel tea. They were weighed daily, and if the rate of gaining weight was not as expected, we additionally provided Zophoba larvae. After fledging, they were moved to an outside aviary at Haidlhof Research Station as a group, together with a sixth individual that was not hand-raised and therefore is not part of the study at hand. Food and water were provided *ad libitum*. Their daily diet consisted of fruit muesli, seeds, fresh fruits and vegetables, and meat, with added variety throughout the week including day-old chicks, eggs, and supplements such as Korvimin, feed lime, garlic powder, and herb blends.

2.2 Data collection

Audio recordings were done in stereo on a handheld recorder (Sennheiser Zoom H4n Pro, sampling rate 48 kHz, amplitude resolution 16 bits) attached to a directional microphone (Sennheiser MKE 600) mounted on a rubber grip with a vibration decoupler. An additional mini-microphone was attached to the second channel of the recorder for annotation purposes. During recording sessions, after a bird vocalised, we recorded the identity of the vocalising bird and the behavioural context in which the vocalisation occurred on this second channel (for a definition of the contexts see Tab. 1). Audio recording took place over two time periods: During hand-raising (Phase 1, i.e. the nestling stage, start: 11-15 days of age, duration: 15 days), and afterwards in an outside aviary (Phase 2, i.e. after fledging, start: 25-29 days of age, duration: 14 days).

2.2.1 Phase 1

During Phase 1, the birds were recorded daily, every two hours between 6 a.m. and 6 p.m. Each recording session consisted of recordings of: (i) five minutes before the start of feeding, (ii) the duration of the feeding session (mean: five minutes and four seconds, range: one minute and 22 seconds to 12 minutes and 34 seconds) and (iii) five minutes after feeding. The birds remained in their nests during the recording and recording sessions were assigned to nests in a pseudo-randomized order, making sure that each nest was featured a similar amount for each of the feeding sessions as well as in a.m. and p.m. recordings each week. Note, however, that not all recordings were included in the analysis.

Table 1: Behavioral contexts and definitions used during audio recordings.

behavioural context	**definition**
beg	beak is open wide, head tilted up, in some cases flapping wings
up	standing / sitting up tall, neck extended
fed	receiving a piece of food by a caretaker
touch - affiliative	being touched on beak or neck by caretaker in a feeding context
touch - aversive	having the beak or head cleaned from food remnants by caretaker
move	caretaker is moving or tapping the nest
disturb	nestmate moves around, resulting in the vocalisation
social	allopreening or bill twining
rest	sitting/crouching/laying down, eyes are open
sleep	crouching/laying down, eyes are closed or head is tucked into feathers
comfort	autopreening or scratching
flight	flight training; flapping of wings two or more times
none	none of the behavioural contexts was recorded for the vocalisation

For details on the annotation and selection process, see section on Audio analysis.

2.2.2 Phase 2

Phase 2 was recorded by my colleague Sara Binder and the resulting data was used with her permission. In Phase 2, the birds were recorded three times a week. Each recording session consisted of (i) a five-minute *ad libitum* recording, (ii) a five minute focal recording of each individual (the order was randomised within sessions), (iii) a five minute *ad libitum* recording. Recording sessions were performed a.m. or p.m. in a pseudo-randomized order (i.e. the ratio of a.m. and p.m. recordings did not exceed 1:2 and alternated each week).

2.3 Audio analysis

All audio analyses were performed in R version 4.4.2 (R Core Team, 2024). The codes for extraction of the call parameters were kindly provided by Anna Osiecka, PhD. The R code for all analyses on individuality was adjusted with permission from Osiecka et al. (2024a).

The obtained audio material was annotated manually in Raven Lite version 2.0.5

(Cornell Lab of Ornithology, 2024) (Phase 1 by thesis author, Phase 2 by my colleague Sara Binder). Calls were selected for extraction and subsequent analysis according to their quality through visual inspection of the spectrograms as well as auditory judgment: only calls which could be clearly assigned to a given individual, had no overlap with calls of other birds or human voice and a high signal-to-noise ratio were selected. For Phase 1, at least one recording of each nest was analysed per recording day. For this, I selected the closest available recording to 12 p.m., as birds were observed to vocalise less in the morning and evening. Where two recordings with the same distance to 12 p.m. were available, I selected the later one, as I observed a slight tendency to vocalise more in the afternoon as compared to the morning. For seven of the 15 days in Phase 1, instead of annotating only one, two to four recordings were annotated for a given nest to obtain a sufficient number of calls for all individuals. Extracted calls were cut to the exact start and end of the audio signal with a custom-made R script based on the callsync package, using the function call.detect (Smeele et al., 2024).

Cut files were batch analysed using the *analyze* function of the *soundgen* package (Anikin, 2019) (pitch floor of 400 Hz, pitch ceiling of 6000 Hz, 1 ms step) to extract a set of spectral parameters of the calls. Only parameters relevant to identity coding across species that could be successfully extracted for all calls were retained for further analysis, leaving eight parameters in total (Tab. 2).

Table 2: acoustic parameters extracted for all calls. definitions as per the *analyze* function manual (Anikin, 2019).

parameter	**definition**
duration (s)	duration of the vocalisation
mean amplitude	mean root mean square of amplitude per frame
peak frequency (hz)	the frequency with maximum spectral power
25th quartile (hz)	the 25th energy quantile of the spectrum
50th quartile (hz)	the 50th energy quantile of the spectrum
75th quartile (hz)	the 75th energy quantile of the spectrum
spectral centroid (hz)	the center of gravity of the frame's spectrum
spectral slope (db/khz)	the slope of linear regression fit to the spectrum

2.4 Statistical analyses

All statistical analyses as well as data preparation were conducted in R (R Core Team, 2025). For data preparation, I used the package dplyr (Wickham et al., 2023). Plots were made using ggplot2 (Wickham, 2016). First, I made separate datasets for calls from the contexts that were featured for each individual in each period. For these as well as the original dataset containing calls from all contexts, I added a column for "period". The periods were defined as following: "nestling - early" (week one of data collection, birds' age at start ranging from 11-15 days and at end from 17-21 days), "nestling - late" (week two of data collection, age at start ranging from 18-22 days and at end from 24-28 days), and "fledgling" (week three and four of data collection, starting with the first day after fledging/being moved out to the aviary, age at start ranging from 25-29 days and at end from 40-44 days).

2.4.0 Principal component analysis

To ensure that factors used for the individuality analyses were not correlated with one another, I performed principle component analyses (PCAs) (one for the pooled data from all contexts and one for datasets from each of the following contexts separately: "beg", "rest", "touch - affiliative" and "touch - aversive". These contexts were chosen based on the fact that each individual was featured with at least six calls for each of them). For all datasets, I first performed a Kaiser-Meyer-Olkin (KMO) test from the EFAtools package (Steiner and Grieder, 2020). The suitability for factor analysis was found to be mediocre, but considering the overall KMO value exceeded 0.6 for all datasets, I decided to proceed with the PCAs, using the "prcomp" function in R. In all cases, scores for the first four principal components (PCs) were retained for further analyses (variance explained: 93% for pooled data; 88% for "beg" data, 95% for "rest" data, 93% for "touch - affiliative" data and 96% for "touch - aversive" data).

2.4.1 Can vocalisations be assigned to the individual based on acoustic parameters?

To investigate whether calls can be assigned to individuals based on their acoustic properties across periods and behavioural contexts, a nested permuted discriminant function

analysis (pDFA, Mundry and Sommer, 2007) was performed on the PC scores from the pooled data. This was done with a nested design including individual as a test factor and context as a restriction factor, using Roger Mundry's function which is based on the lda function of the MASS package (Ripley et al., 2013). In order to examine whether the same was true for each of the three periods, I ran pDFAs for each of them separately (nested design, context as a restriction factor).

To test the individuality of begging calls, a discriminant function analysis (DFA) using the lda function of the MASS package (Ripley et al., 2013) was performed on the PC scores from the dataset containing only begging calls, using individual as a test factor. Since the lowest number of begging calls available for any individual was 37, I selected 37 calls at random for each individual to include in the DFA using the `sample_n()` function from the dplyr package (Wickham et al., 2023) in R. The relative cross-classification level was calculated as the percentage of correct classification by the discriminant function divided by the expected percentage of correct classification based on chance. The significance of the difference between the percentage of correct classification and the expected percentage of correct classification based on chance was determined using Fisher's exact test. To visualise the grouping of calls to the individual, the scores for LD (linear discriminant) 1 of each call were plotted against the scores for LD2, with different individuals appearing in different colours.

2.4.2 Does vocal individuality differ between periods?

To find out whether there is a change in the level of vocal individuality coded in calls pooled from all contexts across the three periods, Beecher's information statistic Hs (Beecher, 1989) was calculated for each period separately. Beecher's Hs measures the level of individuality in a given signal and is considered a robust measure for vocal individuality (Linhart et al., 2019). This was done using the calcHS function from the IDmeasurer package (Linhart, 2019). As the smallest number of calls featured for any individual for any period was 45 calls, I selected 45 calls per individual at random for each period as described under 2.4.1. The same analysis was also run without balancing the number of calls per individual and period to compare the results to the balanced approach.

The same approach as described above was applied to begging calls, but, as six calls

was the smallest number featured for any individual in any of the periods, I selected 6 calls per individual at random for each period using the same function as above. Once again, as the data availability was lowered considerably by balancing the number of calls per individual and period, the same analysis was also run without balancing.

2.4.3 Does vocal individuality differ between contexts?

Using the same approach as seen under 2.4.2, Beecher's Hs was calculated for the pooled data from all contexts and for 4 contexts where enough calls per individual were available (at least five calls per individual; "beg", "rest", "touch - affiliative" and "touch - aversive") separately. However, for this analysis, only calls from the nestling periods were used (pooling them from the early and late nestling period to reach the necessary five or more calls per individual). Since the lowest number of calls available for any individual within any context was seven, I selected seven calls at random for each individual in each context as described under 2.4.1. Once again the same analysis was run without balancing the number of calls between individuals and contexts.

2.4.4 Which acoustic parameters is vocal individuality coded in?

To assess which of the raw acoustic parameters may carry information on the identity of the crows throughout ontogeny, I calculated the potential of individuality coding (PIC; Robisson et al., 1993) for each of the parameters for each of the three periods separately. This was done for the data from the pooled calls as well as the data exclusively from begging calls, using the calcPIC function of the IDmeasurer package (Linhart, 2019). The PIC is calculated by determining the CVb/CVi ratio, CVb being the inter-individual coefficient of variation, and CVi the average of all intra-individual CVs. A PIC of >1 indicates that the corresponding acoustic parameter is individually specific (Robisson et al., 1993).

2.4.5 How does call duration change throughout ontogeny and are there individual differences in this change?

To investigate the change in the duration of begging calls throughout ontogeny and whether there are individual differences in call duration and its change over time, a GLMM

was fitted using the glmmTMB package (Brooks et al., 2017). The full model consisted of duration (in seconds) as a response variable and day (as a proxy for age) and individual as fixed effects along with their interaction term. The model was fitted using a Gamma distribution with a log link function. The model converged and I proceeded to run a series of model diagnostics, namely the diagnostics of the DHARMa package (Hartig, 2024) including tests for dispersion, an outlier test and a chaos test. Furthermore I tested for colinearity of the predictors using the VIF function of the package car (Fox and Weisberg, 2019), applied to a linear model consisting of the response and and the fixed effects without the interaction term. The diagnostics did not suggest any major issues in the fit of the model. This full model was then compared to a null model lacking the test predictors day and individual and their interaction term. Lastly, to assess whether the interaction term improved the fit of the model, the significance of the interaction term was tested using a Chi-squared test.

2.4.6 Individual differences in calling behaviour

To compare how calling behaviour differed between individuals for the three periods, I selected one recording session per recording day for each individual from which to include data (this was done to avoid biases introduced by the fact that for nests with individuals that called less, I annotated more than one recording for some days). The counts of calls from each context was then plotted as a bar plot for each individual separately for each period, with different colours indicating the different contexts. For simplification, I pooled the contexts that were featured under 35 times overall (i.e. ”move”, ”disturb”, ”social”, ”comfort” and ”flight”) with the ”none” context and the ”sleep” context I reassigned to the ”rest” context.

3. Results

3.1 Can vocalisations be assigned to the individual based on acoustic parameters?

Calls from the pooled dataset could be correctly assigned to the individual across contexts and periods significantly above the chance level (nested pDFA, controlling for context: relative cross-classification level = 1.88; p = 0.001; Tab. 3). This stayed true when running separate pDFAs for each period (nested pDFAs, controlling for context: relative cross-classification level = 1.93; 1.96 and 1.94; p = 0.001 for each of them; Tab. 4). The same was the case for begging calls pooled from across the different periods (DFA: relative cross-classification level = 2.30; p = < 0.001; Tab. 5). For a plot of the grouping to the individual along the first two linear discriminants (LD1 and LD2) see Fig. 1.

Table 3: Results of the permuted discriminant function analysis for all contexts and all periods pooled together, controlled for context.

no. context categories	12
total no. calls	2221
correctly classified (%)	36.22
chance level (%)	23.90
p value for classified	0.001
correctly cross-classified (%)	43.20
chance level for cross-classified (%)	22.88
relative cross-classification level	1.88
p value for cross-classified	0.001

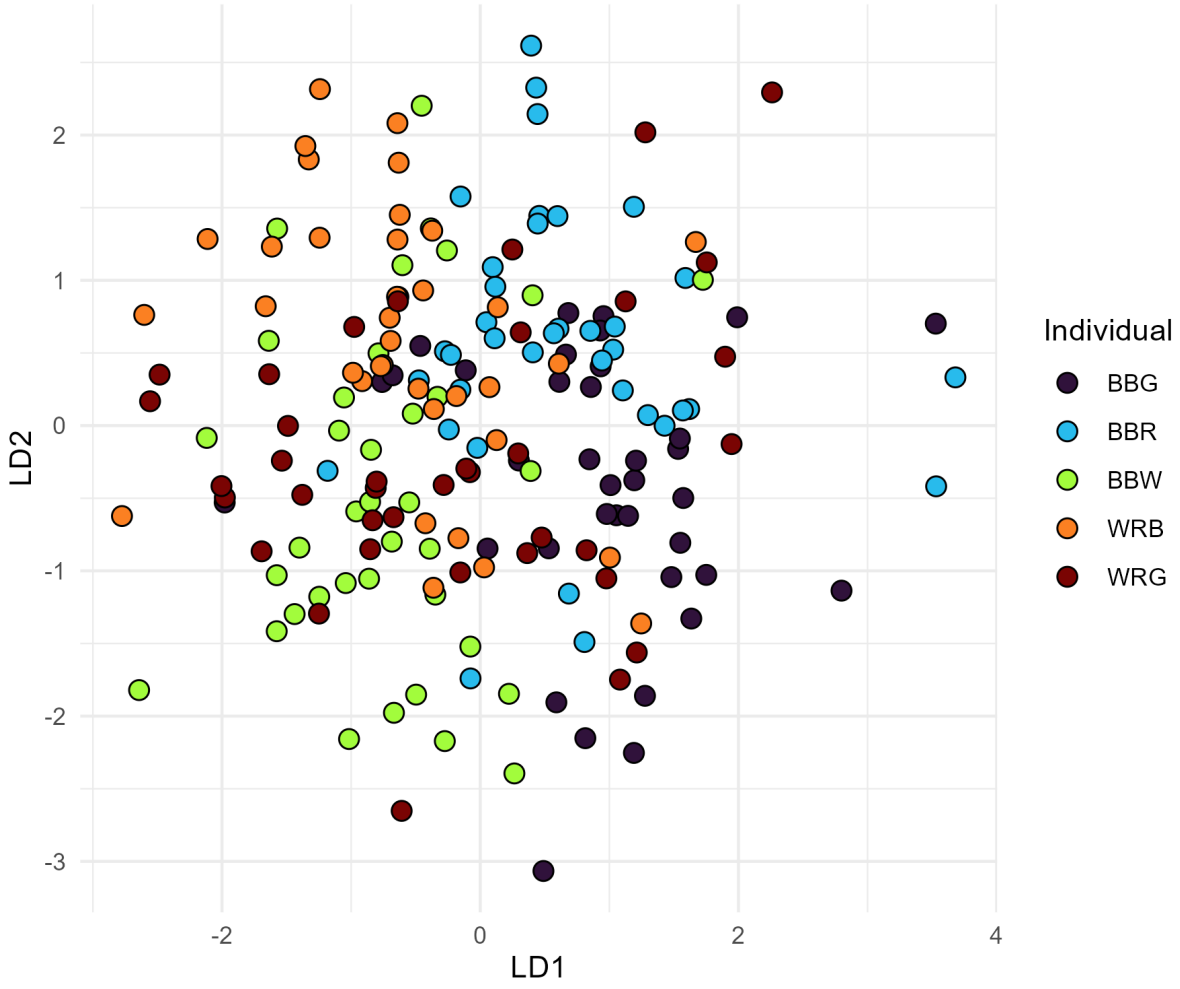

Figure 1: Scores of the discriminant function analysis performed on begging calls, with LD1 (linear discriminant 1) being the linear function that separates individuals best and LD2 (linear discriminant 2) the uncorrelated second most important linear function. Calls from different individuals are shown in different colours.

Table 4: Results of the permuted discriminant function analysis for each period, all contexts pooled together, controlled for context.

result	**nestling - early**	**nestling - late**	**fledgling**
no. context categories	10	11	9
total no. calls	531	689	1001
correctly classified (%)	44.77	45.61	41.95
chance level (%)	25.94	28.13	26.25
p value for classified	0.001	0.001	0.001
correctly cross-classified (%)	48.32	44.83	41.43
chance level for cross-classified (%)	24.99	22.86	21.32
relative cross-classification level	1.93	1.96	1.94
p value for cross-classified	0.001	0.001	0.001

Table 5: Results of the discriminant function analysis for begging calls, all periods pooled together.

total no. calls	185
no. calls per individual	37
correctly cross-classified (%)	45.95
chance level for cross-classified (%)	20.00
relative cross-classification level	2.30
p value for cross-classified	0.00015

3.2 Does vocal individuality differ between periods?

Beecher's Hs values calculated from balanced datasets of calls pooled from all contexts did not indicate a change in vocal individuality across periods, although there was a slightly higher value in the late nestling period (Hs nestling - early = 0.29; Hs nestling - late = 0.48; Hs fledgling = 0.27). For the unbalanced dataset this difference all but vanished (Hs nestling - early = 0.32; Hs nestling -late = 0.37; Hs fledgling = 0.30). Similarly, for the balanced data exclusively from begging calls, Beecher's H values stayed low in all periods (Hs nestling - early = 0.46; Hs nestling - late = 0.50; Hs fledgling = 0.37), thereby not indicating a change in individuality across periods. However, when calculating Beecher's Hs values from the unbalanced dataset, the Hs value of the late nestling period was notably

higher than both for the early nestling and fledgling period (Hs nestling - early = 0.29; Hs nestling - late = 0.95; Hs fledgling = 0.38; Fig. 2). For more figures plotting Hs values for the different periods for the pooled as well as the begging calls, see supplementary material (Fig. 6; Fig. 7; Fig. 8). Call numbers for each individual in each period for the unbalanced approach can be seen in Tab. 9 and Tab. 10 (supplementary material).

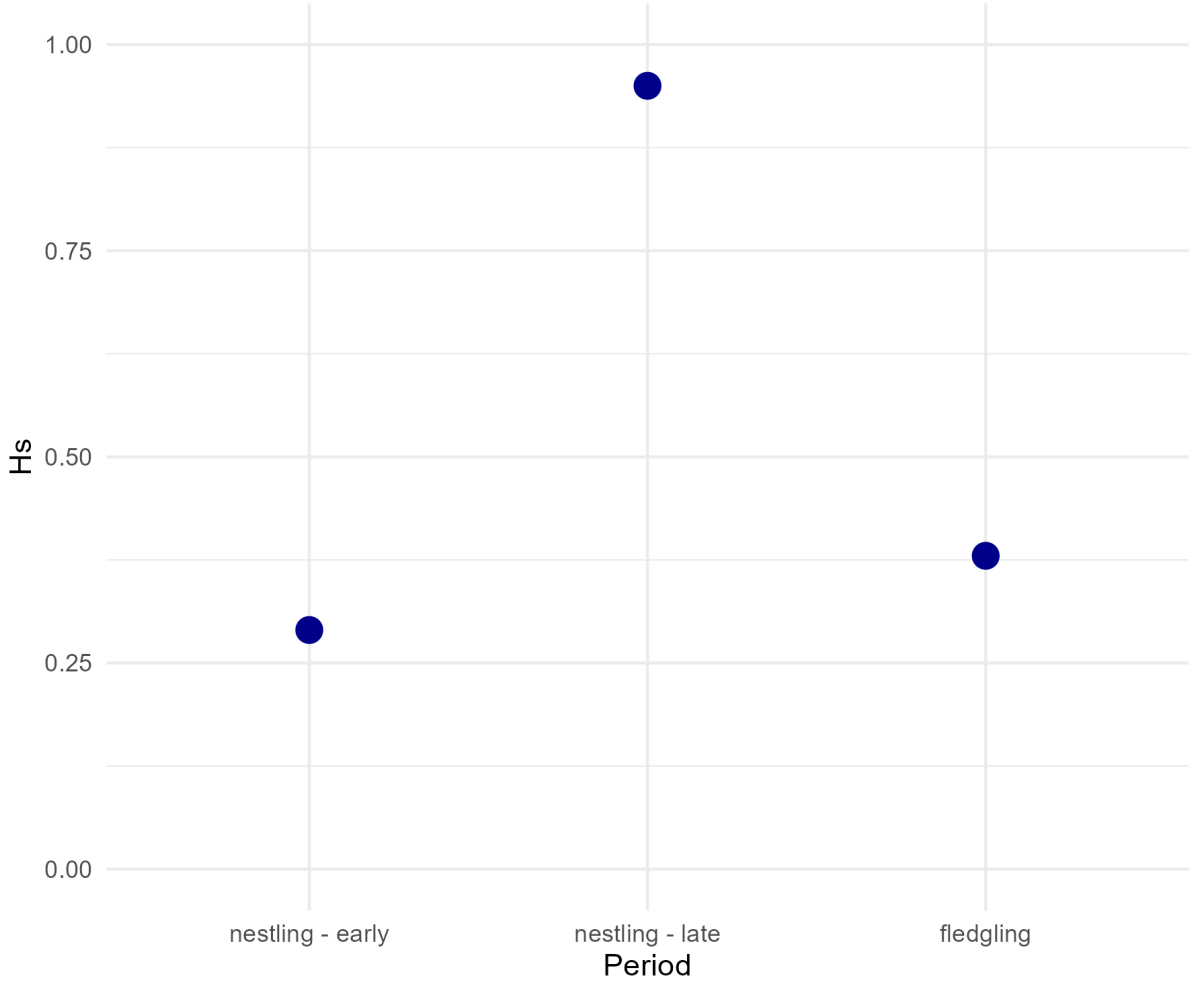

Figure 2: Beecher's Hs values for begging calls from different periods from datasets not balanced for call numbers between individuals and periods. For call numbers, see Tab. 10 (supplementary material).

3.3 Does vocal individuality differ between contexts?

For the balanced dataset, Beecher's Hs values were highest for the "touch - affiliative" and the "touch - aversive" contexts and the Hs value for the data from all contexts pooled together was much lower than the others (Hs for pooled calls = 0.02; Hs for "beg" calls

= 0.46; Hs for ”rest” calls = 0.38; Hs for ”touch - affiliative” calls = 0.64; Hs for ”touch - aversive” calls = 0.56; see Fig. 9 in supplementary material). For the unbalanced dataset, Hs values were noticeably lower for the pooled dataset and for ”rest” calls than for the other contexts, with the Hs value for ”rest” standing out as being particularly low (Hs for pooled calls = 0.36; Hs for ”beg” calls = 0.72; Hs for ”rest” calls = 0.18; Hs for ”touch - affiliative” calls = 0.78; Hs for ”touch - aversive” calls = 0.65; see Fig. 3). For call numbers for each individual in each context, see Tab. 11 (supplementary material).

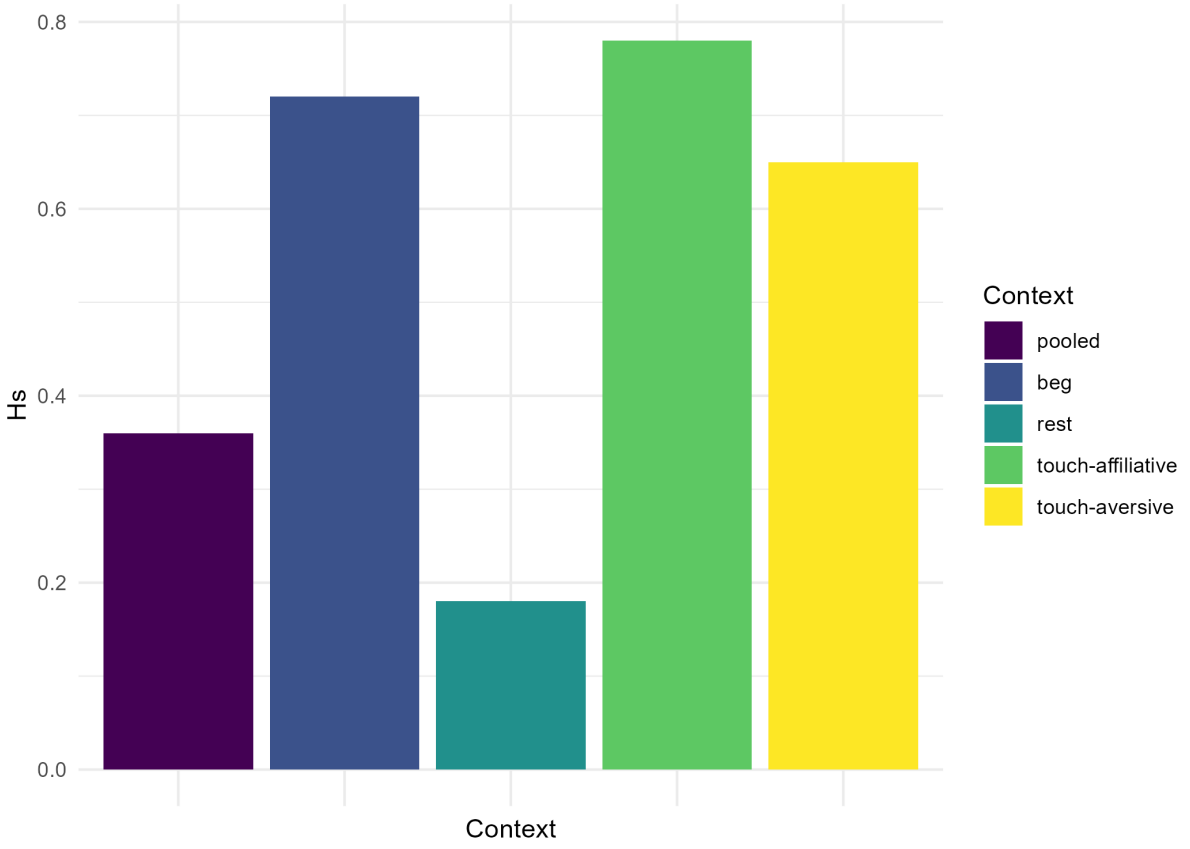

Figure 3: Beecher's Hs values for calls from different contexts from datasets not balanced for call numbers between individuals and contexts. Data was pooled from the early and late nestling period. For call numbers, see Tab. 11 (supplementary material).

3.4 Which acoustic parameters is vocal individuality coded in?

The PIC values for all raw parameters of calls pooled from all contexts suggested an importance for coding individuality in all periods (PIC >1), but none showed particularly

high values of >2 (Tab. 6). The same was true for the raw parameters of calls from the "beg" context (Tab. 7).

Table 6: Potential of identity coding of the extracted acoustic parameters of all call contexts pooled together across the different periods. Values >1 indicate an importance in identity coding.

parameter	**nestling - early**	**nestling - late**	**fledgling**
duration (s)	1.40	1.27	1.13
mean amplitude	1.00	1.01	1.20
peak frequency (hz)	1.00	0.97	1.12
25th quartile (hz)	1.03	0.99	1.08
50th quartile (hz)	1.01	1.06	1.08
75th quartile (hz)	0.98	1.09	1.06
spectral centroid (hz)	0.99	1.07	1.07
spectral slope (db/khz)	0.98	1.03	1.01

Table 7: Potential of identity coding of the extracted acoustic parameters of begging calls across the different periods. Values >1 indicate an importance in identity coding.

parameter	**nestling - early**	**nestling - late**	**fledgling**
duration (s)	1.39	1.50	1.23
mean amplitude	1.00	1.01	1.20
peak frequency (hz)	1.15	1.03	1.21
25th quartile (hz)	1.09	1.06	1.19
50th quartile (hz)	1.12	1.13	1.10
75th quartile (hz)	1.03	1.17	1.03
spectral centroid (hz)	1.10	1.13	1.05
spectral slope (db/khz)	1.02	1.03	1.07

3.5 How does call duration change throughout ontogeny and are there individual differences in this change?

The comparison of the full model to a null model lacking the predictor variables day and individual and their interaction term indicated a significantly better fit of the full model to the data ($\chi^2 = 325.67$; df = 9; $p < 0.001$). The interaction term between day and individual was found to be significant ($p < 0.001$; Fig. 4).

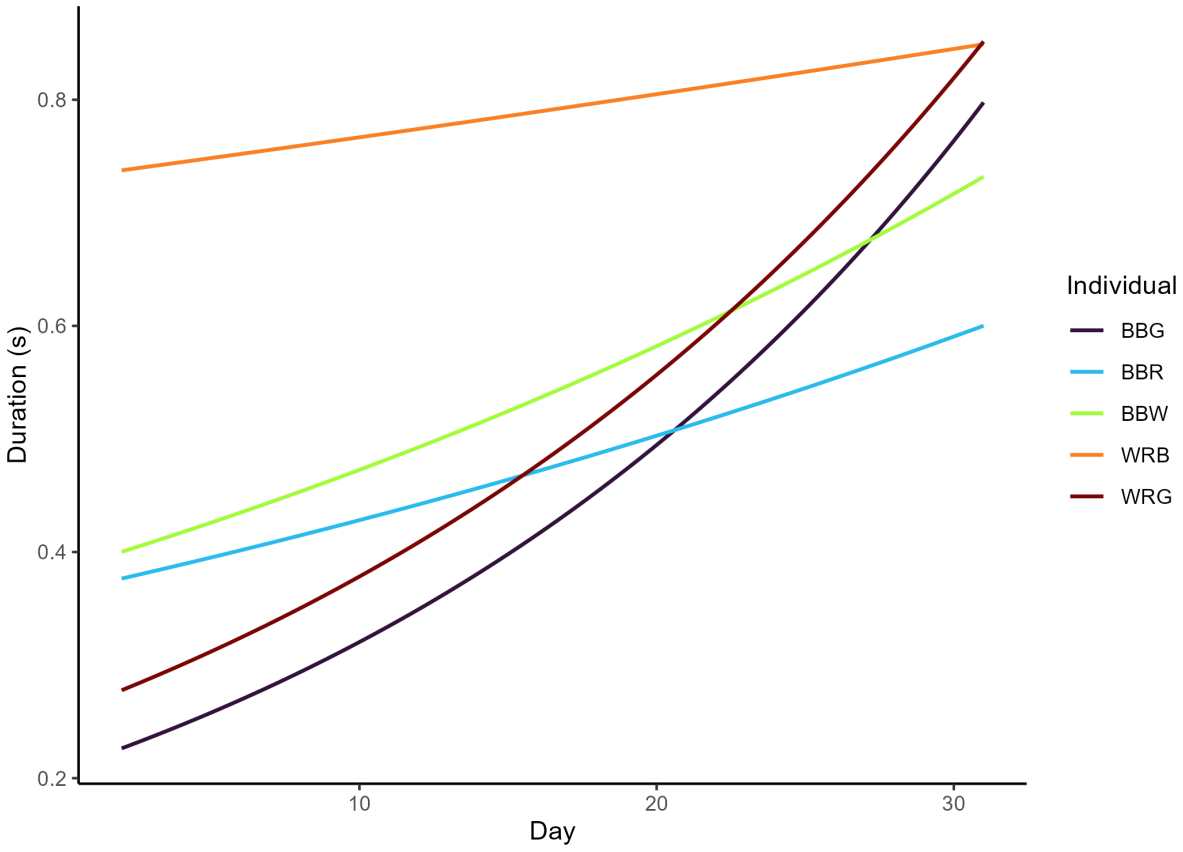

Figure 4: Plot showing the change in the duration of begging calls over time as predicted by the full model. Different individuals are represented by different colours.

3.6 Individual differences in calling behaviour

The total number of calls for each context and period differed between individuals, and which individuals contributed the most calls shifted between periods (Fig. 5).

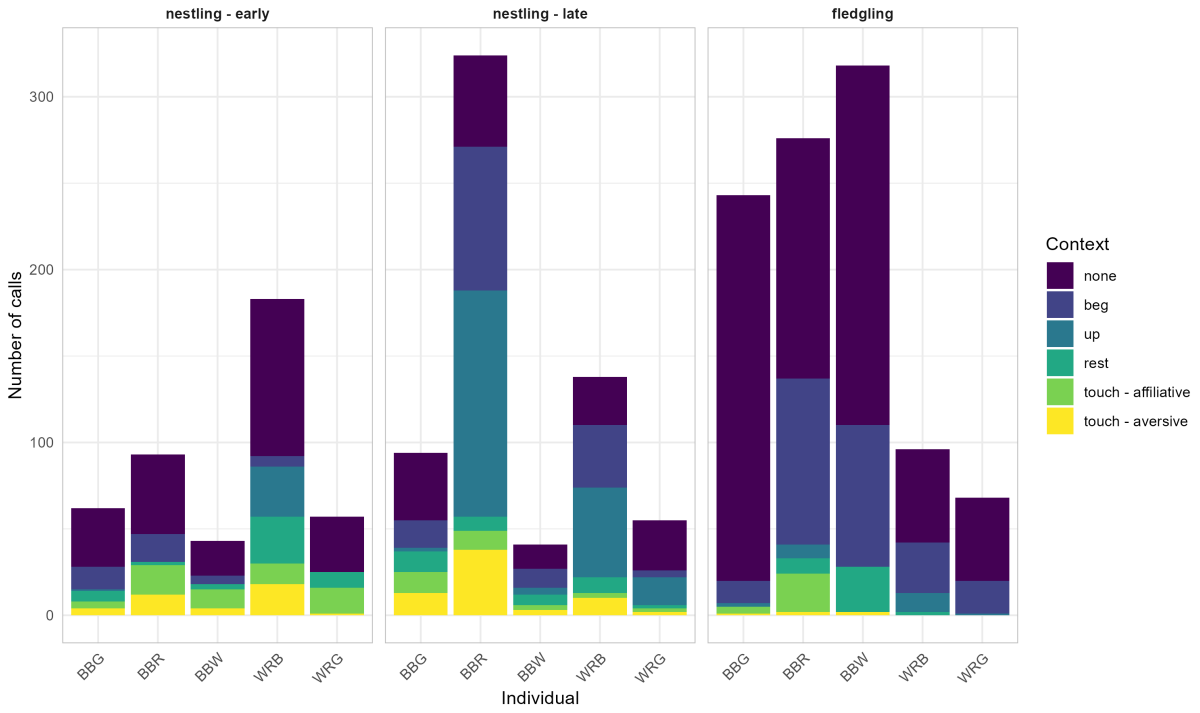

Figure 5: Bar plot showing the total number of calls for each individual across the three periods. Different contexts are indicated by different colours. Data used contained only one recording session per day for each individual.

4. Discussion

Although there is a wide array of studies on vocal individuality in various species (e.g. Charrier et al., 2001; Linn et al., 2021; Smeele et al., 2023; Osiecka et al., 2024a), the factors underlying their development in species of varying life history strategies remain poorly understood. The study at hand is the first to investigate vocal individuality in carrion and hooded crows within the nestling and fledgling stage and thereby contributes to understanding the complex adaptive pressures underlying the development of vocal individuality.

Calls could be correctly assigned to the individual above chance level both across and within periods, showing a presence of vocal individuality from early on in the crows' lives. Beecher's Hs calculations, when not balancing for call numbers, suggested a difference in vocal distinctiveness between different periods as well as between different behavioural contexts. However, these differences were not as clear when limiting call numbers to balance for differences between individuals and periods/contexts. All of the extracted acoustic parameters were found to likely play a role in the underlying identity coding. The development of begging call duration over time varied between individuals and there were also substantial differences between individuals in regards to calling behaviour.

Previous studies on young birds have found vocal individuality cues to be present from very early on in ontogeny. In kea nestlings for example, calls were already individually distinct in the first week after hatching (Wein et al., 2021). Similarly, calls from North African houbara bustard chicks (*Chlamydotis undulata undulata*) could already be correctly assigned for birds of two to five days of age (Cornec et al., 2022). The same has also been found in passerines: A study on zebra finches (*Taeniopygia guttata castanotis*) showed the presence of vocal signatures well before fledging (i.e. at 11 days old, Levréro et al., 2009). Consistent with these results and my prediction, I found that calls could be assigned to the individual above chance level across all periods and across contexts (pDFA

on pooled calls correcting for context). The same was found for each of my established periods, including the earliest period we recorded (the early nestling period, age ranging from 11-21 days). Even though crows are usually territorial breeders and thereby do not run the risk of feeding unrelated conspecifics during the nestling period, they may still profit from individual recognition by voice. Firstly, they can be subject to brood parasites such as the great spotted cuckoo (*Clamator glandarius*) (see e.g. Soler, 1990), so vocal recognition of the chicks may help reject brood parasites (as was found for example in superb fairy wrens, *Malurus cyaneus*, Colombelli-Négrel et al., 2012). The chicks may furthermore use sibling recognition based on vocal cues of identity in negotiations for parental resources, as has been hypothesized for barn owl nestlings (Dreiss et al., 2014). Future studies could investigate whether crow chicks can in fact individually discriminate between their nestmates' vocalisations (likely the case in barn owls, see Ruppli et al., 2013).

The DFA for calls only from the begging context for a balanced number of begging calls per individual performed only slightly better than the pDFA for calls pooled from all contexts (relative cross-classification level 2.30 and 1.88, respectively). Begging calls have been hypothesized to not only serve as an identity signal towards parents, but also towards nest-mates, likely improving brood cohesion after fledging (Ligout et al., 2016). Both functions may be relevant to our crows. It may be beneficial for vocal identity cues to be present before fledging, so that parents (and nest-mates) can learn to recognize chicks' voices (as suggested e.g. by Levréro et al., 2009, for begging calls of zebra finches).

Some previous studies have shown a change in vocal individuality through ontogeny. For instance, Brittan-Powell et al. (1997) found that the calls of Budgerigars (*Melopsittacus undulatus*) become easier to discriminate with increasing age of chicks, whereas in chicks of north african houbara bustards, contact calls appeared to become less individually distinct with age (Cornec et al., 2022). According to the authors, this decrease in vocal individuality follows a parallel decrease in the adaptive value of being individually recognizable, owing to an increased independence of chicks as they start to search for food on their own. In this thesis I predicted an increase in vocal distinctiveness of begging calls following a hypothesized increase in its adaptive value owing to a higher mobility of the crows after fledging, as well as an approaching transition to a socially more complex life in a non-breeder group. Interestingly, when not balancing for call numbers between

individuals and periods, Beecher's Hs was highest for the intermediate period (the last week before leaving the nest, Hs = 0.95 as compared to Hs = 0.29 for the early nestling and Hs = 0.38 for the fledgling period). This result was not in line with my prediction, as I expected the value to be lowest in the early nestling period, intermediate in the late nestling period and highest in the fledgling period. It is possible that the transition from living inside to being moved out to the aviary caused considerable stress on the chicks. Previous studies have shown that affective state can influence vocal individuality: In little auks, the vocal individuality of calls uttered when handled by a human was lower than in interactions with parents in the nest. In this regard, it was suggested that the higher entropy (i.e. noisiness or harshness) of the calls produced in the handling context may lead to a loss of information on identity coded in spectral parameters (Osiecka et al., 2024b). Generally speaking, it has been proposed that narrow band harmonic calls may be better suited to conveying individual identity when compared to more broad-band noisy calls (e.g. Yin and McCowan, 2004; Leliveld et al., 2011). The begging calls of our crows appeared to become more noisy close to and after fledging (personal observation), gradually resembling more adult-like calls, which could theoretically have contributed to a decay of individual identity. However, the potential of individuality coding (PIC) of frequency measures did not decrease in the fledgling period. Future studies should quantify this change in noisiness to shed more light on a possible role it may play in individuality coding. Another factor that could come into play is the fact that the fledgling period spanned double the time than the other two. If the birds went through considerable developmental and subsequent vocal changes in these two weeks, this may reduce the apparent individuality when pooling calls from this whole time frame. More research with bigger datasets is needed to shed light on this hypothesis. It is important to note that when balancing the call numbers between individuals and periods, there was no such pattern in the individuality of calls. This is in accordance with the results Levréro et al.'s 2009 study on zebra finch chicks, which also found no change in individuality of begging calls over time and explained the early presence of vocal signatures with a need of the parents to familiarize themselves with their chicks' signatures before fledging. However, as the overall call number was reduced considerably by the balanced approach in my study (only 30 calls in total per period), this result may not reflect the actual situation. On the other hand, the result for the unbalanced dataset may reflect the fact that a lot more data

was available for the later two periods than for the first (56 for the early nestling stage, 160 for the late nestling stage and 235 for the fledgling stage), although this could likely only account for the difference in Hs values between the two nestling stages rather than the difference between the late nestling and the fledgling period found in the unbalanced dataset. Ideally, future studies would have more data to balance call numbers between birds and periods while retaining a sufficiently large sample. For the calls pooled from all contexts, there was a slightly higher value in the late nestling period (Hs = 0.48) compared to the other two (Hs for nestling - early = 0.29, HS for fledgling = 0.27) in the balanced approach. Here, the number of calls remained rather high, at 225 total calls per period. The result may thereby be more trustworthy than the one from the balanced dataset of begging calls. With the unbalanced dataset, the Hs values remained similar between periods (Hs values ranging from 0.30 to 0.37). The generally low values (all Hs < 0.50) are perhaps unsurprising, as the analysis approach does not include a control for context / call types, so the apparently low individuality may simply be due to calls from different contexts being pooled together.

Previous studies on vocal individuality have typically focused on one distinct call type (e.g. Aubin and Jouventin, 2002; Kondo et al., 2010; Dentressangle et al., 2012), but works across repertoires are also available, with results showing a different degree of vocal individuality depending on call types, likely owing to their different communicative functions and the need for individual recognition in a given interaction (e.g. bonobos, *Pan paniscus*, Keenan et al., 2020; white rhinoceroses, *Ceratotherium simum*, Linn et al., 2021 and plain zebras, *Equus quagga*, Xie et al., 2024). Comparable studies have been conducted on bird species as well: In little auks, calls could be assigned above chance levels to individuals within as well as across call types, with certain call types containing more information on individual identity than others (Osiecka et al., 2024a). Similarly, in south polar skuas (*Stercorarius maccormicki*), the potential of individuality coding (PIC) was found to be high in contact and courtship calls, but only weak in alarm calls (Charrier et al., 2001) and in zebra finches, contact calls show strong individual signatures while calls during aggressive interactions are not as individually distinct (Elie and Theunissen, 2018). Typically, these studies have divided calls into call types. I instead focused on the behavioural contexts in which vocalisations took place, as call types are yet to be established for nestlings and fledglings of carrion and hooded crows. In line with the

social function hypothesis (as expanded by Lemasson and Hausberger, 2011), I predicted the highest level of individuality (as measured by Beecher's Hs) for begging calls and other calls from affiliative contexts, an intermediate level for calls from aggressive/aversive contexts and the lowest level for calls related to general activities or not directed towards specific individuals. Not balancing call numbers between individuals and contexts, I found considerable differences in the individuality of calls from different contexts. The lowest Hs value resulted from calls emitted in the "rest" context (Hs = 0.18), fitting well with my prediction. These vocalisations took place while a bird was lying or crouching down with open eyes, a behaviour which I defined as resting, consequently representing a context related to general activities. Apart from the Hs value for calls pooled from all contexts, the other values all exceeded 0.60, with calls from the "touch - affiliative" context showing the highest level of individuality (Hs = 0.78), followed closely by the begging calls (Hs = 0.72) and lastly the calls from the "touch - aversive" context (Hs = 0.65). Even though the Hs values only differ slightly, these results partly fit my hypothesis, with the calls from the aversive context (in which the birds had their beaks cleaned by a caretaker and would usually attempt to pull away) resulting in the lowest Hs value, possibly reflecting a negative emotional valence of the situation. If begging calls do in fact serve as the basis for adult vocalisations (see e.g. Sawhney et al., 2006), they might be subject to more changes in structure throughout nestling development than other call types. Their measured level of individuality could therefore be affected more strongly by pooling calls from both nestling periods (two weeks in total). Furthermore, as the acoustic parameters of begging calls are known to shift with hunger (e.g. Reers and Jacot, 2011), they may be more variable than calls from the "touch - affiliative" context, although more studies are needed to confirm whether calls from the "touch - affiliative" context (which are emitted in response to a gentle touch on the head or beak to elicit begging) are affected by hunger as well.

The calculation of the PIC for the call parameters suggested the importance of multiple parameters (Tab. 6, Tab. 7) in identity coding for both the begging calls and the calls pooled from all contexts, and this stayed true throughout the three periods. While all of the parameters' PIC values were close to 1.0 (suggesting an importance in identity coding), none of the PIC values reached especially high values exceeding 2.0. The parameters found to potentially serve an identity function span both the frequency, the

temporal and the amplitude domain. Studies on other species found similar results insofar as identity is frequently coded by a combination of acoustic parameters spanning different acoustic domains (e.g. Searby et al., 2004; Levréro et al., 2009; Osiecka et al., 2024a). As suggested by Osiecka et al. (2024a), information coded by multiple domains of sound is less likely to be lost through transmission and coding identity through a variety of parameters may therefore be adaptive. Furthermore, some of the parameters commonly important in conveying identity information (such as duration or maximum frequency) may change with development, suggesting that a multiparametric way of coding identity could be more reliable when it comes to parents correctly identifying their chicks (Marques et al., 2011). Levréro et al. (2009) found that only a combination of parameters enabled a discriminant function to correctly assign calls to individuals, indicating that parents' ability to use information from a combination of parameters is necessary in order to discriminate between chicks. To investigate what parameters crow parents use for individual recognition, playback experiments with experimentally altered chick vocalisations are needed.

In my thesis, begging call duration served as an example of a parameter that is important both in individuality coding (e.g. Reers and Jacot, 2011; Wein et al., 2021; Osiecka et al., 2024a) and is known to change over development (e.g. Marques et al., 2011; Teixeira et al., 2022). In line with my predictions, begging call duration increased with chick age and this change was individualized (Fig. 4). The increase may well represent a shift towards more adult-like vocalisations, as was discussed for other species in previous studies (e.g. Marques et al., 2011; Teixeira et al., 2022). Further studies on shifts in the repertoire of crows through ontogeny are needed to shed light on the role of begging calls in the development of the adult repertoire. Regarding individual differences, there was one individual (WRB) that stood out in particular, starting with a call duration similar to / higher than the one the others reached at two weeks post-fledging. This calls into question the interpretation I suggested in my prediction, namely that an increase in call duration is made possible by a larger lung capacity with increasing age. As chick weight was monitored during hand-raising, I checked whether individual WRB stood out in that regard. WRB started out as the second heaviest with 291 g (range 242-304 g) and by the end of the first week had become the third heaviest with 316 g (range 265-388). It therefore seems unlikely that size was the factor explaining the higher call duration of

this chick early in development. Future studies should ideally have larger sample sizes and control for additional measures of chick development (such as plumage and mobility) to address this issue. As call duration has also been found to signal hunger (e.g. Sacchi et al., 2002; Leonard and Horn, 2006; Marques et al., 2008), future studies on hand-raised birds could incorporate measures of food consumption to see whether such individuals with longer call durations early in life are simply signaling a greater need for food. The theory of WRB signaling more hunger in the early stage of the nestling period could be supported by the observations I made on individual differences in calling behaviour (i.e. the number of vocalisations produced), as calling rate is known to be another signal of hunger in nestlings (e.g. Leonard and Horn, 2006), and WRB was the individual contributing the highest overall number of calls in the early nestling period (Fig. 5).

In the study at hand, I found big individual differences in the calling behaviour in every one of the three periods (Fig. 5), both regarding the overall call numbers as well as in the ratio of calls from different behavioural contexts. Which individual contributed the highest number of calls shifted between periods. As the sample size of five individuals is rather small, interpretations of these differences are still somewhat speculative. Previous studies have shown that calling rate of nestling may signal nestling quality. This can even be call type specific: In Atlantic puffins (*Fratercula arctica*), chicks in good condition emit more peep-calls, while those in poor condition emit more screech-calls (Rector et al., 2014). A study on spotless starling nestlings (*Sturnus unicolor*) found a decrease in the begging effort for chicks subjected to an immune challenge (Parejo-Pulido et al., 2024). This may also have played a role in the consistently low call number of individual WRG, which was sick during the hand raising period and gained weight at a slowed rate. The development of call numbers for individual BBW may also point towards interesting questions for future research: This individual was removed from its biological siblings, and instead shared a nest with two other chicks it was not related to (WRB and WRG) as part of another study. It showed the lowest total number of calls in both nestling periods, but the highest number of calls in the fledgling period. Future research could therefore focus on the social aspects influencing calling rates in young crows. The number of calls may reflect different attributes in different life stages of the crows. In adult jungle crows, calling rate has been found to be related to dominance (N. Kondo and Hiraiwa-Hasegawa, 2015). This may have played a role in the fledgling period of our study. Future studies

may want to investigate whether such an effect exists in carrion and hooded crows and at which life stage this effect comes into play.

Although the study at hand can serve as a starting point for investigations into the development of vocal individuality in carrion and hooded crows, it comes with some limitations that future studies may want to address. Firstly, the sample size of five individuals would ideally be increased in follow-up studies and it may be beneficial to include data from more than one year of chicks to account for differences in environmental conditions between years, thereby leading to more generalisable results. Future studies could also profit from a bigger number of calls being available for each behavioural context. Secondly, we did not control for calls stemming from sequences, which may have lead to the intraindividual variation of calls being underestimated in our analyses: In monk parakeets (*Myiopsitta monachus*), calls of a given individual stemming from the same recording were found to be more similar, especially when produced right after one another (Smeele et al., 2023).

As the individuality of vocalisations can differ depending on arousal (e.g. Keenan et al., 2020; Osiecka et al., 2024b; Corvin et al., 2024), differences in individuality coding throughout development may simply reflect different affective states due to a change in holding conditions rather than a changing adaptive value of being individually distinct. Incorporating physiological measurements of stress or arousal could help disentangle these factors. For this study, we separated calls into contexts rather than call types. While this approach allowed looking at context-dependent variations in vocal individuality, future research may profit from establishing call types for nestlings and fledglings of carrion and hooded crows.

Lastly, the crows in our study were hand-raised from 10-14 days of age onward. Although this ensured high quality of recordings, it also means that the vocal development of our crows may not accurately reflect natural conditions. We tried to minimize this issue by housing our crows as a group and exposing them to vocalisations of wild and captive adult crows through open windows during the nestling stage. Even so, future studies may consider including recordings from crow nests in the wild.

Despite these limitations, the study at hand represents a first look at the development of vocal individuality in carrion and hooded crows, thereby contributing to our understanding of the different factors of life history (such as physical development, social

environment, and shifts in this environment throughout an animal's life) that can affect vocal individuality cues. Not only did it show the presence of vocal individuality throughout the nestling and the early fledgling period of crows, but also a possible shift in the level of individuality with age in begging calls, as well as with behavioural context. One of the next steps will be to investigate how crow parents and possibly siblings use this information on individual identity through playback and cross-fostering experiments.

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6. Supplementary Material

Table 8: Data on individuals including estimated hatching dates, estimated age at the start of phases 1 and 2, original and artificial nest numbers, nest types, and sex.

individual	hatching date	age p1	age p2	original nest	artificial nest	nest type	sex
BBR	2024-04-21	10	25	MA1	1	natural	m
BBG	2024-04-21	10	25	MA1	1	natural	m
BBW	2024-04-21	10	25	MA1	2	paper	f
WRG	2024-04-17	14	29	AN1	2	paper	f
WRB	2024-04-17	14	29	AN1	2	paper	f

Table 9: Number of calls used for calculations of Beecher's H for different periods, unbalanced between individuals and periods.

individual	nestling - early	nestling - late	fledgling
BBG	78	94	243
BBR	95	324	276
BBW	70	45	318
WRB	215	155	96
WRG	73	71	68

Table 10: Number of begging calls used for calculations of Beecher's H for different periods, unbalanced between individuals and periods.

individual	**nestling - early**	**nestling - late**	**fledgling**
BBG	13	16	13
BBR	16	83	96
BBW	7	13	82
WRB	14	36	29
WRG	6	12	19

Table 11: Number of calls used for calculations of Beecher's H for different contexts in the nestling stage, unbalanced between individuals and contexts.

individual	**pooled**	**beg**	**rest**	**touch-affiliative**	**touch-aversive**
BBG	172	29	15	16	17
BBR	419	99	10	28	50
BBW	115	20	12	17	7
WRB	370	50	36	16	29
WRG	144	18	12	18	7

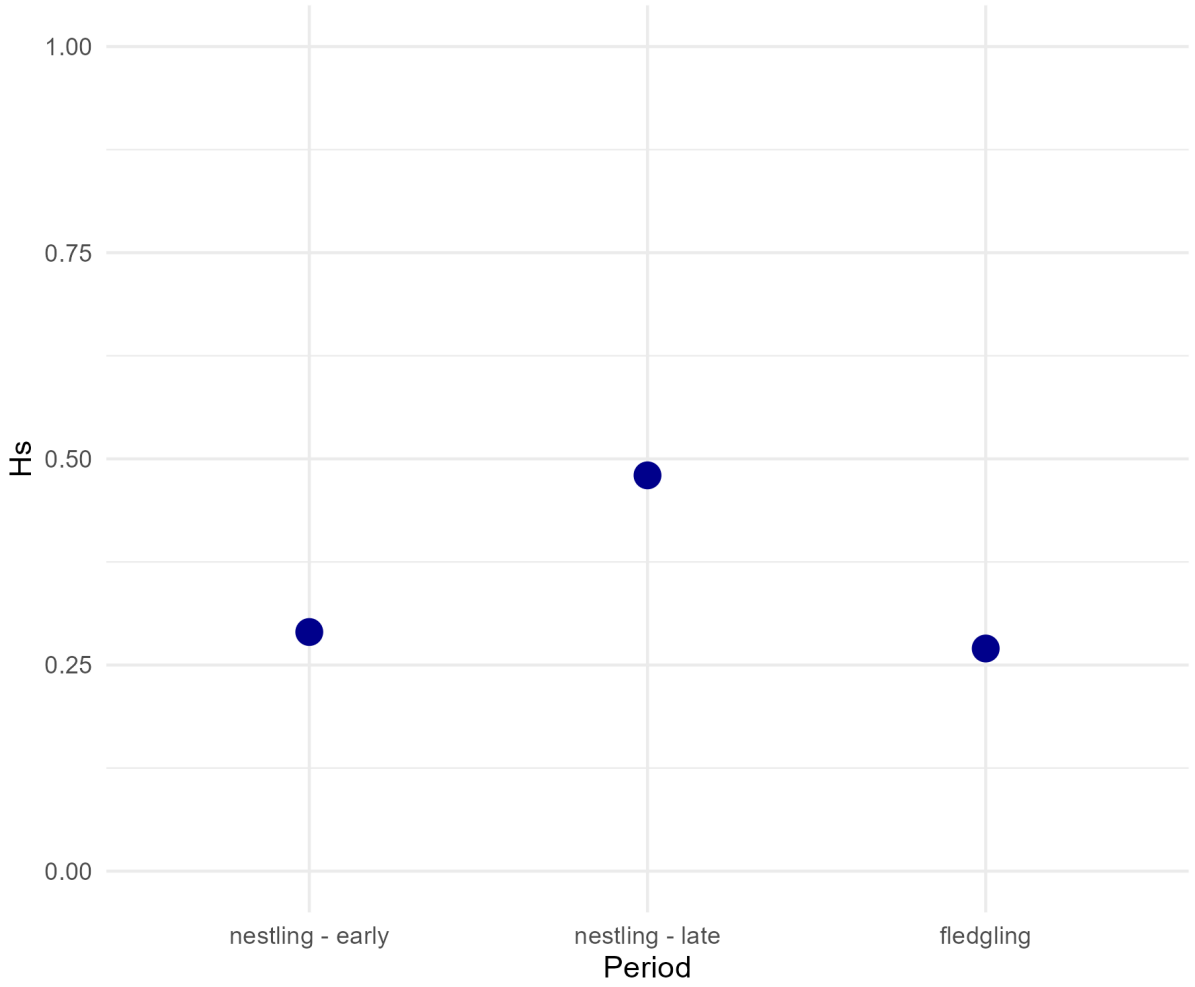

Figure 6: Beecher's Hs values for calls from different periods from datasets balanced for call numbers between individuals and periods (45 calls per individual for each period).

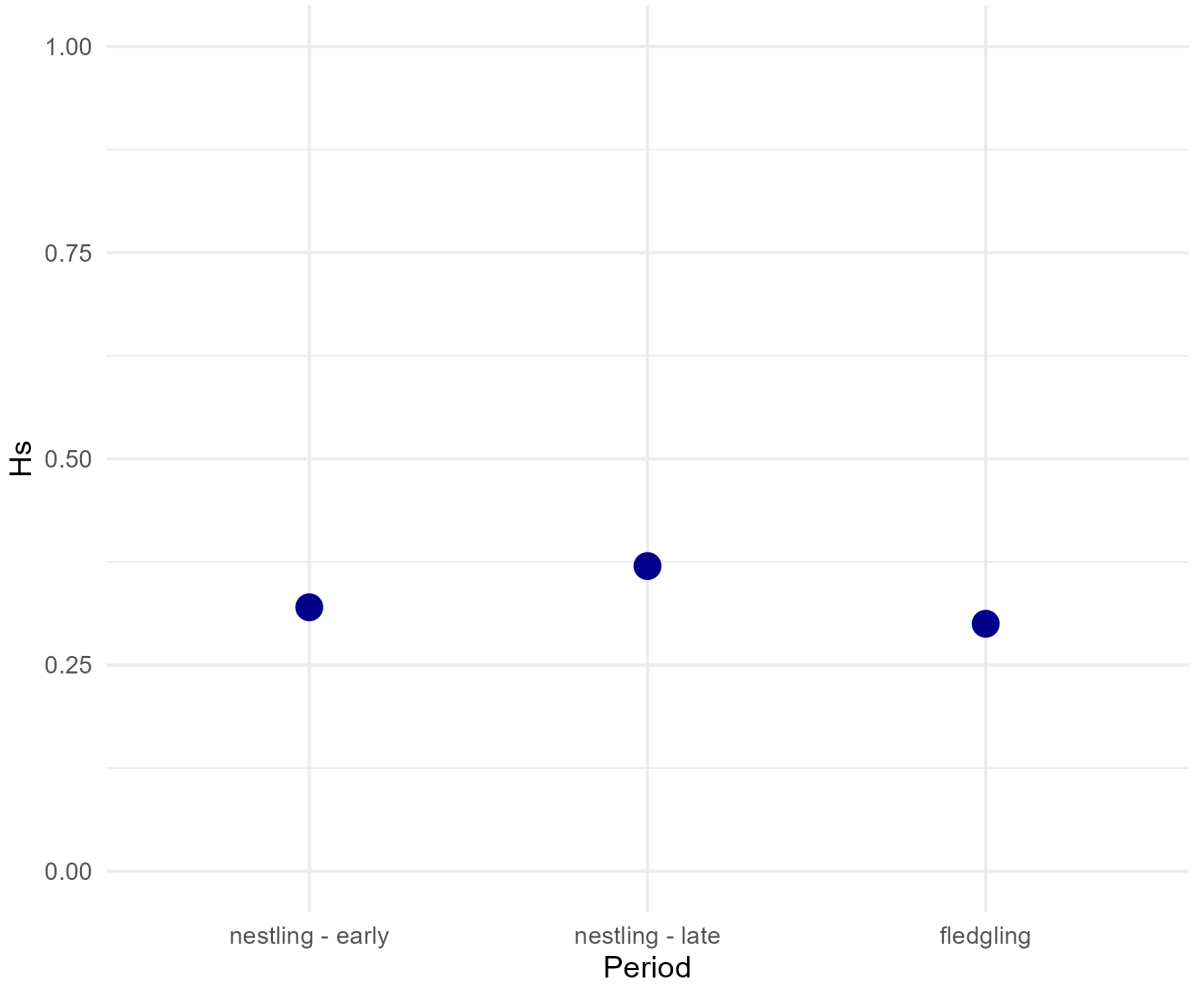

Figure 7: Beecher's Hs values for calls from different periods from datasets unbalanced for call numbers between individuals and periods. For call numbers, see Tab. 9.

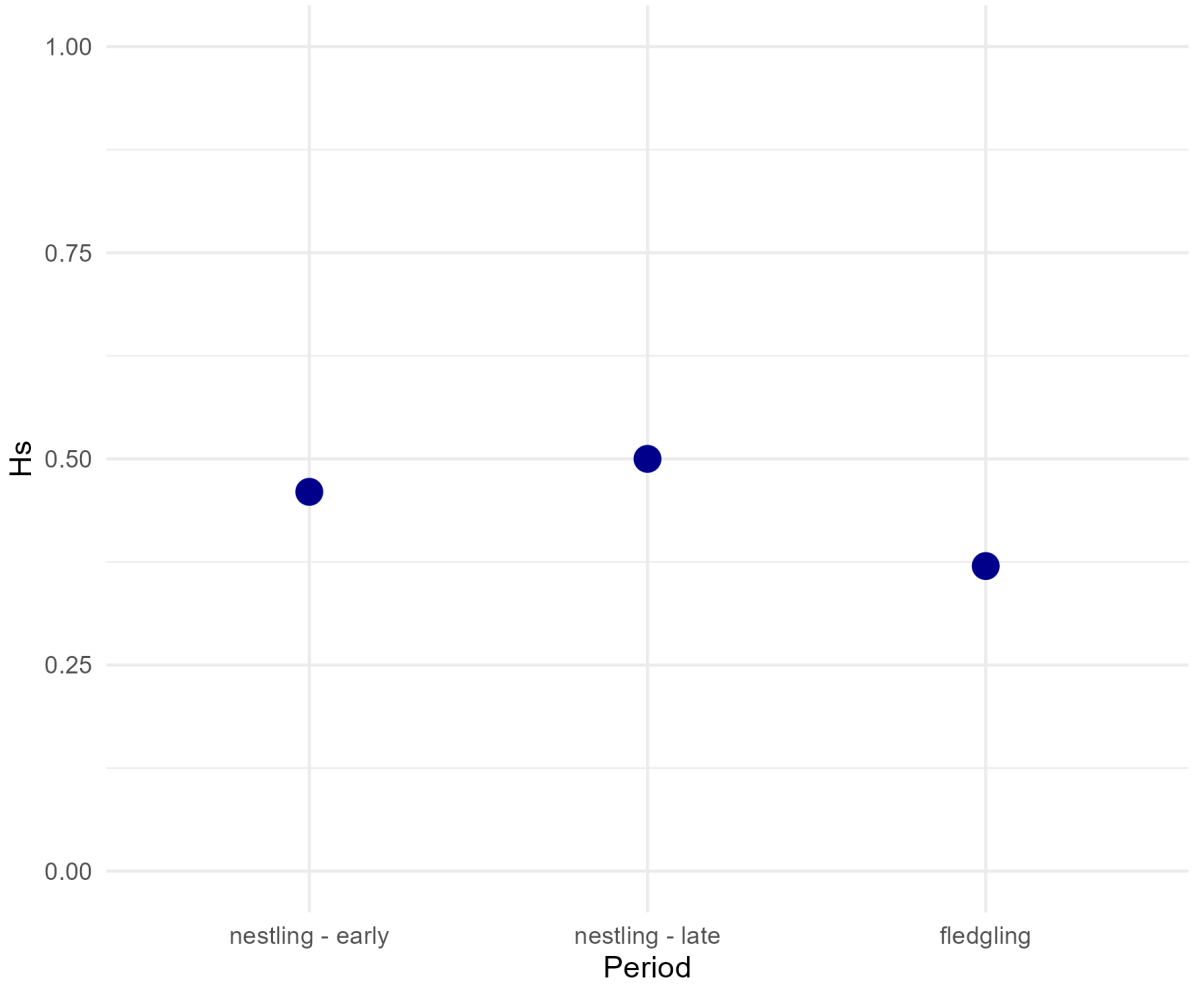

Figure 8: Beecher's Hs values for calls from different periods from datasets of begging calls balanced for call numbers between individuals and periods (six calls per individual for each period).

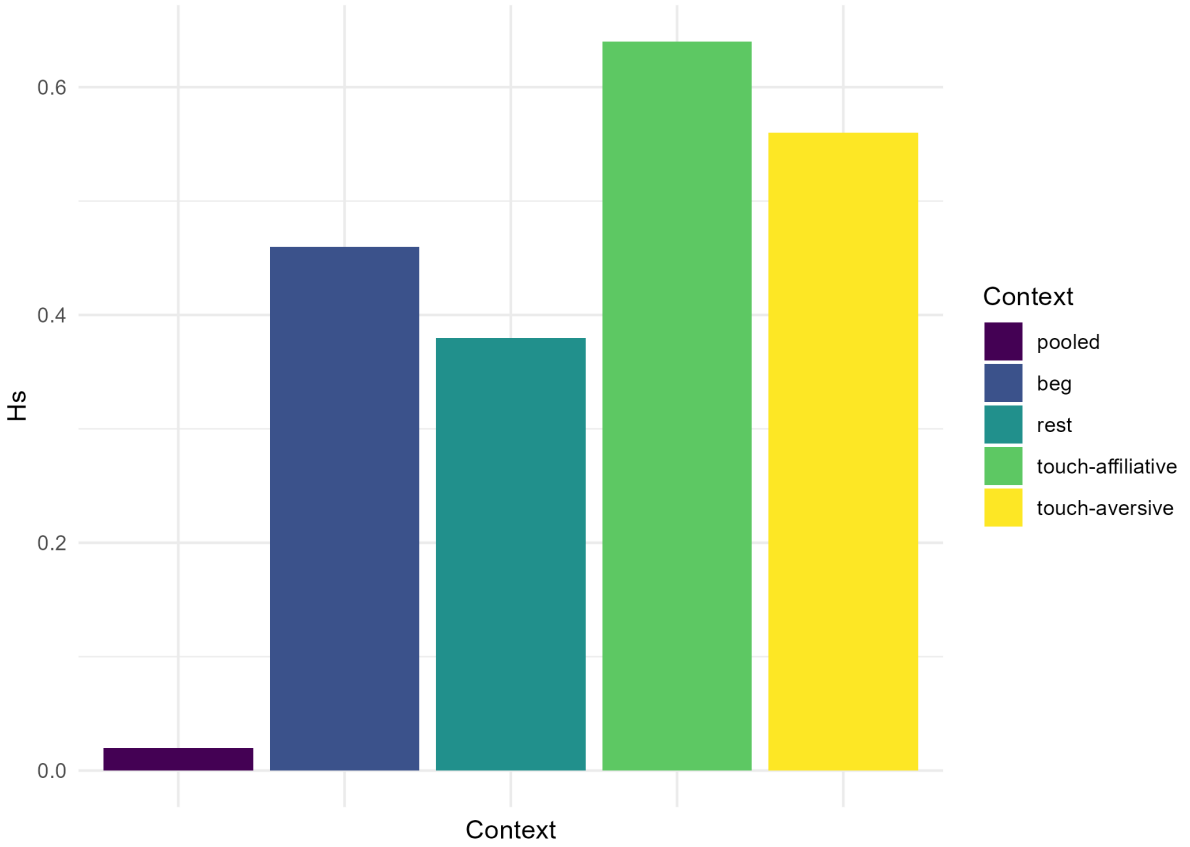

Figure 9: Beecher's Hs values for calls from different contexts from datasets balanced for call numbers between individuals and contexts (seven calls per individual for each context) . Data was pooled from the early and late nestling period.

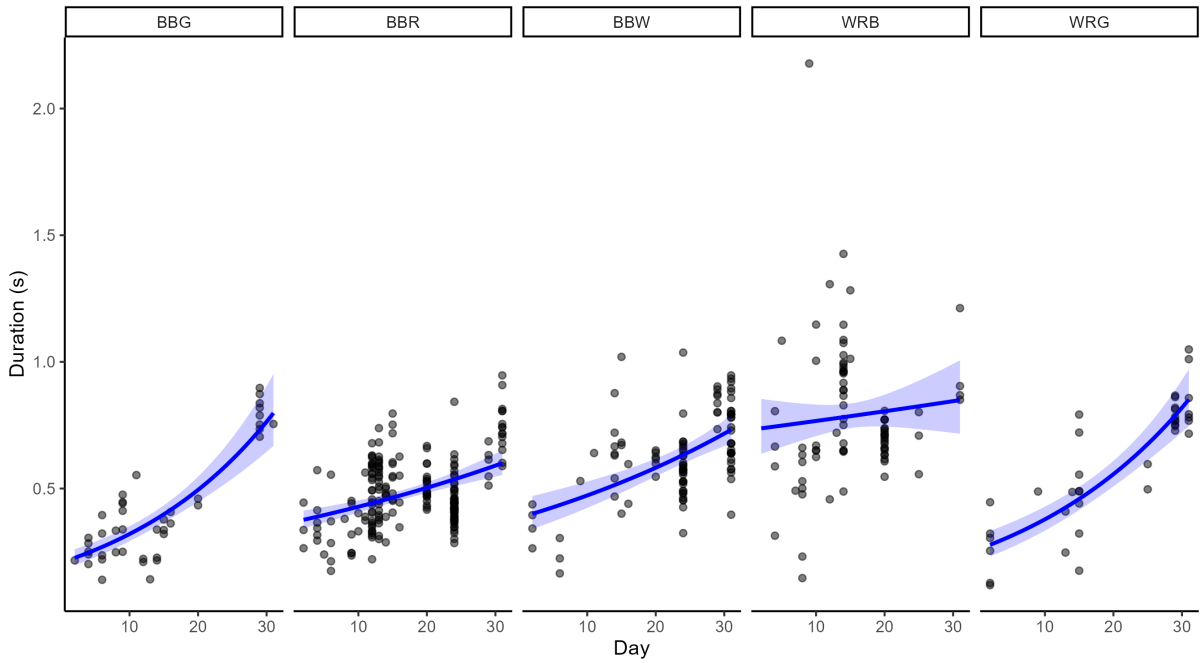

Figure 10: Fit of the full GLMM containing duration of begging calls as a response and day (as a proxy for age) and individual as well as their interaction term as fixed effects, with confidence intervals shown as ribbons. Observations of begging call durations are shown as opaque points.