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Individuality in houbara chick calls and its dynamics throughout ontogeny

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ABSTRACT: In many taxa, breeding success depends heavily on reliable vocal recognition between parents and offspring. Although the acoustic basis of this recognition has been explored in several species, few studies have examined the evolution of acoustic cues to identity across development. Here, in a captive breeding program, we investigated for the first time the acoustic signals produced by North African houbara bustard *Chlamydotis undulata undulata* chicks. Two call types (contact and distress) were recorded from 15 chicks in 4 age classes. Acoustic analyses showed that the acoustic parameters of the calls varied systematically with age in both contact and distress calls. However, both call types remained highly stereotyped and individualized between chicks at every tested age, indicating that calls encode reliable information about individual identity throughout development, thus potentially enabling the mother to distinguish her own chicks through their development up to fledging. Playback experiments are now needed to verify such parent–chick recognition in houbara bustards and its efficiency across chick ontogeny.

KEY WORDS: Acoustic communication · Individual recognition · Houbara bustard · Contact call · Distress call

1. INTRODUCTION

Individual recognition between parents and offspring is crucial for maintaining parent–young bonds, for selective feeding and for avoiding misdirected expensive parental care, thus ultimately preventing fitness costs and increasing breeding success (Beecher 1981). Parent–offspring recognition has been documented in many taxa, including mammals (Bohn et al. 2007, Charrier et al. 2009, Pitcher et al. 2010, Knörnschild et al. 2013, Sibiryakova et al. 2015), reptiles (Main & Bull 1996, Bull et al. 1999) and birds (passerines: Leonard et al. 1997, Draganoiu et al. 2006, Levréro et al. 2009; non-passerines: Lefevre et al. 1998, Charrier et al. 2001, Clark et al. 2006).

This ability is particularly relevant for most bird species where chicks are wholly dependent on adults for food, warmth and protection against predators. During early life stages, when recognition is most critical for a chick's survival, parent–chick recognition accuracy appears to reach a peak and may decrease or cease when young acquire independence (Lefevre et al. 1998).

In birds, the coding strategies to signal individual identity are closely related to the species' biology (colonial or solitary/territorial, synchronous or asynchronous nesting, precocial or altricial chicks, gregariousness and mobility of the young, family size) and to the difficulty of the recognition task. For example, the relevance of parent–chick recognition

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is vital when visual cues are insufficient or absent, allowing parents or chick(s) to locate one another and when the risk of misidentification is high (Beecher 1991, Barg & Mumme 1994, Mathevon et al. 2003, Benedict 2007). A series of playback experiments in penguins, examining behavioural responses in parents and chicks, showed that non-nesting species use more complex call structures to encode individual identity (king penguin *Aptenodytes patagonica* and emperor penguin *A. forsteri*) relative to other nesting penguin species (e.g. gentoo penguin *Pygoscelis papua*, Adelie penguin *P. adeliae*, rockhopper penguin *Eudyptes chrysocome*) (Aubin et al. 2000, Lengagne et al. 2000, 2001, Aubin & Jouventin 2002, Searby et al. 2004). In colonial swallow species, chicks develop individually distinctive signature calls prior to fledging, a vocal signature used by the parents to distinguish their own young (Beecher 1981, Stoddard & Beecher 1983, Loesche et al. 1991).

The recognition process between parents and young can rely on a variety of communication modalities, including acoustic, visual and olfactory cues (Ruiz-Miranda 1993, Nowak et al. 2000). However, in numerous species, the recognition process depends mostly on acoustic signals, which are an efficient sensory modality for long-range communication (Catchpole & Slater 2008). As shown in mammals, reliable vocal identification cues often arise from inter-individual differences in the vocal apparatus, including vocal tract length, that impose honest (reliable) anatomical constraints on call parameters (Taylor & Reby 2010, Briefer & McElligott 2011). Throughout ontogeny, the vocal apparatus constantly changes in size with chick development and body growth (Volodin et al. 2007). The development of the vocal organ is thus likely to be reflected by modifications to the acoustic parameters of the chick's calls, until the acquisition of mature vocal patterns. For example, in some bird species without vocal learning (e.g. common shelduck *Tadorna tadorna*, Engländer & Bergmann 1990; pied avocets *Recurvirostra avosetta*, Adret 2012), certain vocal frequencies (peak frequency and fundamental frequency, for example) steadily decrease throughout development, while for other species, frequency parameters remain relatively stable until fledging or chick independence (Klenova et al. 2007, 2010, Duckworth et al. 2009, Klenova & Kolesnikova 2013). Vocal parameters may also depend on the sex of the chick in species where sexual dimorphism in vocal anatomy emerges early (Radford 2004). Finally, even in species considered to be non-vocal learners such as some Galliformes species, plasticity of call parameters during development as a function of social or emotional

factors has been demonstrated (Derégnaucourt et al. 2009, Desmedt et al. 2020). Thus, individual signatures based on vocal parameters that change over time may pose a problem for parent–chick recognition over long periods (Dale et al. 2001, Tibbetts & Dale 2007). The evolution of individual signatures during chick ontogenesis (maintenance or alteration) and its potential effects on the parent–chick recognition process has remained largely underexplored.

In the North African houbara bustard *Chlamydotis undulata undulata* (hereafter houbara), acoustic traits (booming calls) are strong components of the adult male's courtship behaviour. These calls have been shown to carry information about the male's individuality and are related to his physiological, physical, genetic and behavioural traits (Cornec et al. 2014, 2015, 2019). Unlike for adults, no study has yet examined vocalizations produced by houbara chicks or the ontogeny of these vocalizations. Houbara chicks are precocial and leave the nest within only a few hours of hatching (Collar 1996). After leaving the nest, chicks (1–4 chicks per brood; Gaucher 1995) follow the mother, who raises the brood alone. Chicks are fully dependent on maternal care for food and protection against predators (Collar 1996). This dependency remains until the young are fully fledged, around 60 d after hatching, at which stage the young begin dispersing (Hardouin et al. 2012). The chicks produce 2 main call types, contact calls (CC) and distress calls (SC), in different behavioural contexts (Collar 1996, C. Cornec pers. obs.). The CC encourages cohesion among siblings and between chicks and their mother. It also elicits the mother's feeding behaviour (authors' pers. obs.). The SC is typically produced when a chick is fully isolated without visual contact with its mother or when the chick feels threatened (authors' pers. obs.). Individual recognition between mother and chicks is expected to avoid expensive misdirected parental care. Indeed, due to an aggregated spatial distribution of the nests (Hingrat et al. 2008), chicks of different broods might intermingle freely in the same area. Thus, considering the expected importance of individual recognition throughout the development of the chick to maintain mother–offspring relationships, we investigated the individuality in CCs and SCs in houbara chicks and the dynamics of these calls along individual ontogeny. We predicted that vocal parameters will vary systematically with age and weight but that despite these intra-individual changes, both call types are predicted to retain inter-individual signatures throughout ontogeny, allowing for continuous individual and kin recognition.

2. MATERIALS AND METHODS

2.1. Subjects and animal housing

Recordings were performed in 2012 on captive birds produced at the conservation breeding of the Emirates Center for Wildlife Propagation (ECWP; Morocco). Reproduction was based on artificial methods to enhance production and genetic management: collection of semen, insemination of females, incubation of eggs and hand-rearing of young (Saint Jalme & Van Heezik 1996, Lesobre 2008). Two categories of birds are produced in the facility: future breeders, to renew the breeding flock, and release birds, used for conservation translocation (Rabier et al. 2020). To avoid imprinting, birds destined for release have limited contact with humans, and therefore our study subjects included only future breeders due to experimental procedures involving repeated human contact. After hatching, future breeders are kept for 10 d in heterosexual groups (5 chicks per group) in a box (50 × 40 × 20 cm) and are fed manually by humans. At 30 d old, birds are placed in individual outdoor cages (2 × 2 × 2 m). Food and water are provided ad libitum, with a diet composed of pellets, mealworms, crickets, animal proteins and fresh alfalfa. The chicks are sexed through DNA analysis and individually marked with rings. All birds in our study were born between 10 and 14 April 2012. To avoid any potential confounding sex-effects that might arise from sexual dimorphism during growth, only males were selected for the recordings.

2.2. Ethical note

The birds used in the captive breeding part of the study were artificially bred in agreement with the 'Ministère de l'Agriculture, Développement Rural et des Pêches Maritimes, Direction Provinciale de l'Agriculture de Boulemane, Service Vétérinaire' (Nu DPA/48/285/SV) under permit No. 01-16/VV; OAC/2007/E; Ac/Ou/Rn. Bird handling and measurements were performed by trained bird keepers or doctors of veterinary medicine employed by the ECWP to minimize any adverse effects (e.g. stress, trauma).

2.3. Data collection

A total of 15 chicks were recorded 4 times each between the ages of 2 and 46 d: Age 1: 2–5 d; Age 2: 14–15 d; Age 3: 30–31 d; Age 4: 43–46 d.

The 2 main vocalizations produced by houbara chicks (CCs and SCs) were recorded while each chick was isolated for a short time (<15 min) in a box without any visual or vocal interactions with other chicks. Vocalizations were recorded using a Gras 46AE microphone (frequency response: 3.15 Hz – 20 kHz, ±2 dB) connected to a Marantz PMD661 recorder (frequency response: 20 Hz – 24 kHz, ±1 dB; sampling frequency: 44.1 kHz). To elicit CCs, chicks were in visual contact with the bird keeper and were stimulated by presenting them with food (mealworm given with a clamp). To elicit SCs, chicks were kept alone without any external stimulation. Then, the microphone was presented, either handheld (CCs) or mounted on a tripod (SCs), at head height and less than 1 m from the chick. In most cases, the isolation of the chick very quickly led to the production of SCs. We aimed to obtain at least 10 CCs and 10 SCs per bird and per age category. If more than 10 calls were recorded per bird per age, we randomly selected 10 calls for analysis among those of good signal-to-noise ratio. If an insufficient number of calls was obtained during a session, we reorganised another session on another day to avoid keeping the chick isolated for too long. To achieve enough calls, the average number of recording sessions was 1.25 ± 0.45 per chick per age, with a maximum of 3 d separating 2 sessions for one chick at a given age. We failed to obtain 10 CCs for 2 birds at Age 3 and 10 SCs for 1 bird at Age 4; these birds were not included in the analyses for those age classes.

Chicks in each age class were weighed before the recordings using an electronic scale (±1 g precision).

2.4. Acoustic analysis

Only high-quality recordings with high signal-to-noise ratios, not disrupted and non-overlapped by external noise (wind, other bird calls, human voice) were analysed, using Avisoft-SASLab Pro (R. Specht, v.4.40; Avisoft Bioacoustics). Prior to analysis, audio files were filtered to remove background noise (high pass: 500 Hz). Temporal parameters were measured on waveforms, and frequency parameters were measured on spectra.

2.4.1. Contact calls

A CC consists of a sequence of mildly frequency-modulated pure tone sound units separated by intervals of silence (Fig. 1). Some units contain a 2-voice

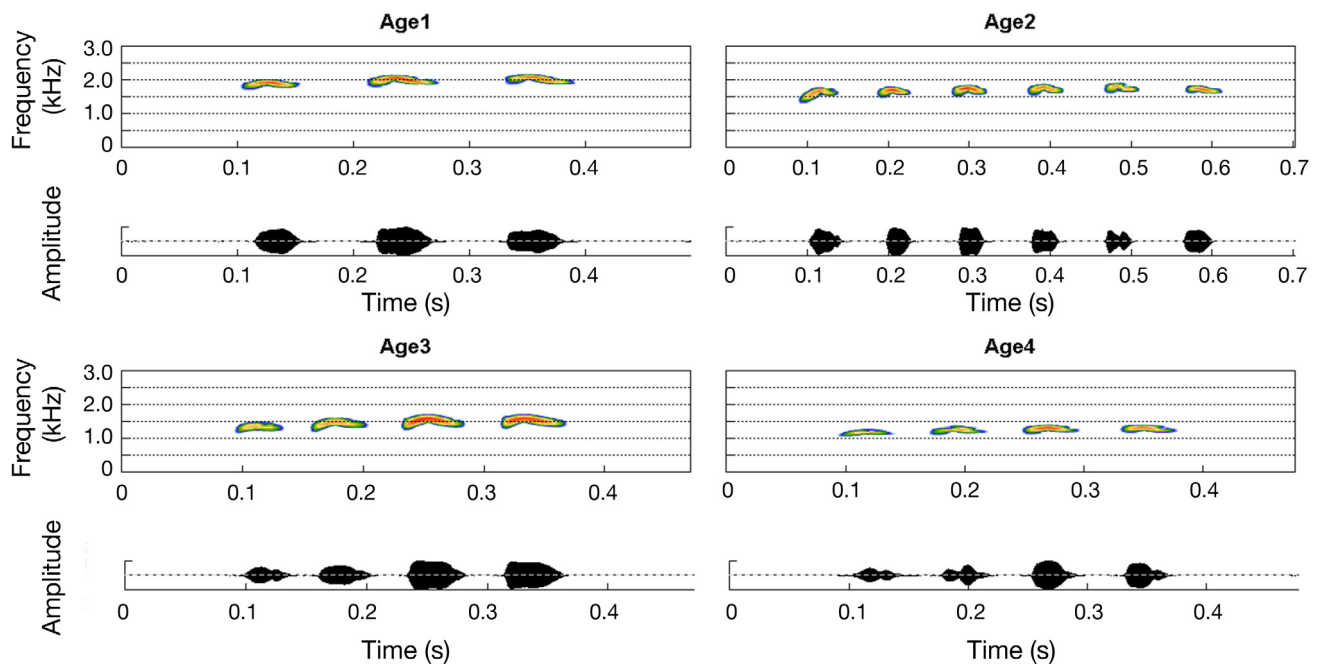


Fig. 1. Spectrograms and oscillograms of contact calls produced by a North African houbara bustard *Chlamydotis undulata undulata* chick at different ages (Age 1: 2 d; Age 2: 15 d; Age 3: 30 d; Age 4: 43 d). Hamming window; fast Fourier transform window size: 1024 pts; 90% overlap (figures made with Seewave; Sueur et al. 2008)

phenomenon (2 simultaneous series of related bands of slightly different frequencies; Aubin et al. 2000, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n047p061_supp.pdf). This phenomenon was observed in 21% of CCs (Table S1).

For each CC, 5 temporal parameters were considered, and on the second unit of each CC, 7 frequency parameters were measured (Table 1).

2.4.2. Distress calls

An SC is a single, mildly frequency-modulated, pure tone sound unit (Fig. 2). A 2-voice phenomenon was observed in 38% of SCs (Table S1, Fig. S2).

For each SC, 1 temporal parameter and 4 frequency parameters were measured (Table 1).

We used the 'scan frequency contour' option of Avisoft to extract the fundamental frequency at 21 regular time intervals from the 1st voice and

Table 1. Acoustic parameters of contact calls (CC) and distress calls (SC) of North African houbara bustard chicks. (*) Frequency parameters

	Parameter description	Acronym
Contact call	Duration of the entire sequence	DSCC
	Duration of the second unit	DUCC
	Duration of silence interval between 2 units ^a	DIUCC
	Number of units per sequence	NUCC
	Tempo ^b	TCC
	Fundamental frequency of the 1 st voice* ^c	F01CC
	Fundamental frequency of the 2 nd voice* ^c	F02CC
	Frequency gap* ^d	GCC
	Quartile 25%*	Q25CC
	Quartile 50%*	Q50CC
	Quartile 75%*	Q75CC
	Energy below 1500 Hz*	E1500CC
Distress call	Duration of the call	DSC
	Fundamental frequency of the 1 st voice* ^c	F01SC
	Fundamental frequency of the 2 nd voice* ^c	F02SC
	Frequency gap* ^d	GSC
	Mean fundamental frequency of the 1 st voice*	MF0SC

^aDuration of each silence between 2 successive units within the same sequence
^bTCC was estimated by calculating the ratio NUCC/DSCC
^cMeasured over a window of 0.1 s where the signal energy level is at its maximum
^dGCC and GSC were estimated by calculating respectively the differences F02CC - F01CC and F02SC - F01SC. When the 2nd voice was absent, GCC or GSC were equal to zero

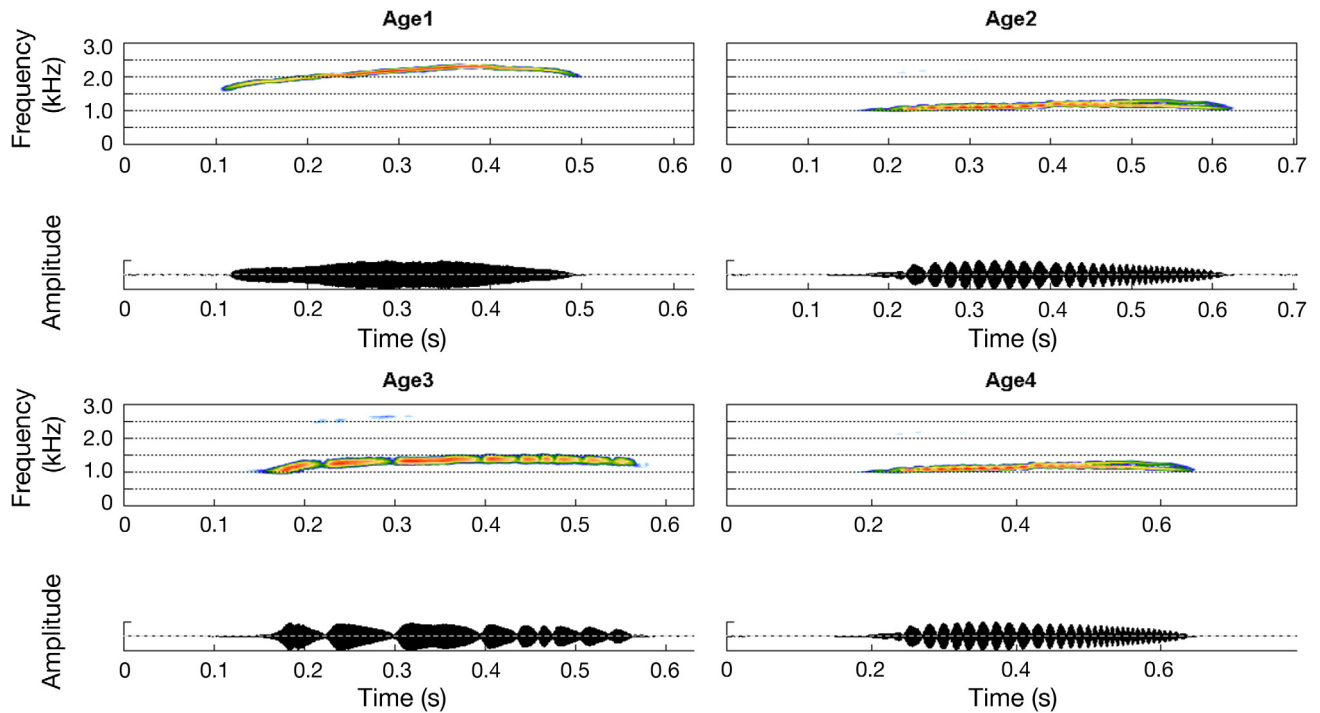


Fig. 2. Spectrograms and oscillograms of distress calls produced by a North African houbara bustard *Chlamydotis undulata undulata* chick at different ages (Age 1: 2 d; Age 2: 15 d; Age 3: 30 d; Age 4: 43 d). Hamming window; fast Fourier transform window size: 1024 pts; 90% overlap (figures made with Seewave; Sueur et al. 2008)

averaged these measures to obtain the mean fundamental frequency of the 1st voice (MF0SC).

2.5. Statistical analysis

All statistical analyses were conducted using STATISTICA v.6.1 (StatSoft 2001) and R v.3.6.1 (R Core Team 2019); results are presented as means \pm SD (see Table 2). All tests were 2-tailed with the significance level set at $\alpha = 0.05$. We performed Kolmogorov-Smirnov tests to verify that the distributions of acoustic parameters did not depart significantly from Gaussian ($p > 0.05$).

First, we calculated the potential for individual coding (PIC) for each acoustic parameter. This was assessed by calculating the CV_b/CV_i ratio, where CV_b is the inter-individual coefficient of variation and CV_i is the average of all intra-individual CVs (Robisson et al. 1993). All CVs were calculated after correcting for small sample sizes: $CV = (SD/m) \times (1 + [1/4n])$, where SD is the standard deviation, m is the mean of the given individual and n is the number of calls for a given individual (Sokal & Rohlf 1981). For a given acoustic variable, $PIC > 1$ indicates that this variable is individual-specific because the intra-individual

variability is smaller than the inter-individual variability (Robisson et al. 1993). $PIC > 2$ has a high probability for individual coding (Scherrer 1984).

To test whether vocalizations could be reliably classified according to the identity of their emitter, we used discriminant function analysis (DFA), which compares variation among individuals across several levels simultaneously. To optimize the DFA, we selected the acoustic parameters with the highest PIC values and excluded collinear parameters. Seven acoustic parameters measured from CCs (3 temporal and 4 frequency parameters) and 3 measured from SCs (1 temporal and 2 frequency parameters) were included in these analyses. For the SC at Age 1, the frequency gap (GSC) was not included in the analysis because all measurements for this parameter were equal to zero. We also performed a cross-validation DFA using the cross-validation leave-one-out method to assess the reliability of the DFA results. In order to reduce biases associated with scaling, all values were standardized using the Fisher z-transformation. DFAs were performed using the R package 'MASS' (Venables & Ripley 2002).

We also conducted 2 series of generalised linear mixed models (GLMMs) using the 'lmer()', 'lme()' and 'glmmTMB()' functions of the 'lme4', 'nlme' and

'glmmTMB' packages (Brooks et al. 2017, Kuznetsova et al. 2017, Pinheiro et al. 2021). Due to an excess of 0 values in the data, we applied a negative binomial or Tweedie distribution for the frequency gaps of CCs and SCs (GCC and GSC) using the function 'glmmTMB()'. Models were run using an identity link function with a Gaussian distribution. For some acoustic parameters, logarithmic transformations were applied to achieve normality of residuals. For each mixed model, we report 95% CIs and p-values.

The first set of GLMMs tested for relationships between acoustic parameters and chick weight at each age and for both calls. Chick weight was included as a fixed effect and chick identity was included as a random effect in all GLMMs. This first series of models allowed us to (1) check to what extent the investigated acoustic parameters were affected by weight within each age class and (2) test for a link between individual acoustic signature and weight. To achieve this latter goal, whenever a significant relationship between weight and an acoustic parameter was detected, repeatability and adjusted individual repeatability of the acoustic parameters were quantified using the functions 'rpt()' of the package 'rptR' (Stoffel et al. 2017) and compared. Adjusted repeatability corresponds to the fraction of the total variance in the population that can be attributed to variation among individuals while controlling for the variance explained by the fixed effect weight. Repeatability was assessed with the 'rptR' package, as it allows estimation of CIs based on parametric bootstrapping associated with the repeatability estimates ($n = 1000$ data samples). When the effect of weight was not significant, we assessed individuality based solely on the PIC previously computed.

We then conducted a second series of models complementary to the first. Here, we aimed to test for the effect of chick age on the acoustic parameters of CCs and SCs. Chick age (range: 2–46 d) was systematically included as a continuous fixed effect, and chick identity was included as a random effect. Weight was not included in this series of models due to its high correlation with age ($r = 0.95$), thus avoiding collinearity problems. Based on preliminary data exploration, the relationship between some of the acoustic parameters and chick age was non-linear; thus, we ran second- or third-order polynomial models. Here, the tempo measures were fitted using a beta regression (Douma & Weedon 2019). Finally, we thoroughly assessed the models' assumptions regarding normality of residuals, homoscedasticity and temporal independence of repeated individual measures to decide on refinements of the

models. We detected temporal autocorrelation and heteroscedasticity in residuals. Consequently, in all models, we specified autocorrelation functions to model temporal dependencies and allowed variance to change with age (Pinheiro & Bates 2000). All models were fitted using the 'lme' function of the 'nlme' package. However, we could not assess the significance of the repeatability using the 'rptR' package for these complex models. Therefore, we have only provided the adjusted repeatability estimates. Finally, to further evaluate individual consistency in call parameters across age, we calculated Pearson pairwise correlations between age-specific mean individual acoustic parameters.

3. RESULTS

In total, we analysed 580 CCs (3798 call units) and 590 SCs. General descriptions of acoustic parameters are given in Tables 2 & 3.

3.1. Individuality of the calls

For all acoustic parameters of the CC (except for energy below 1500 Hz [E1500CC] at Age 2), inter-individual CVs were significantly higher than intra-individual CVs at every age, and 9 temporal and frequency parameters had PIC values higher than 2 for at least one age (Table 2, Fig. S3), indicating a high probability for individual coding in call structure. Interestingly, the highest PIC values were measured for temporal parameters in the 2 first age categories (Age 1 and Age 2), whereas the highest PIC values were measured for frequency parameters in the last 2 age categories (Age 3 and Age 4).

All acoustic parameters of SC at every age were highly individualized, based on high PIC values (Table 3, Fig. S3).

The cumulative percentage of the first 3 functions of the DFA explained 82–97% of the total variance of the CC parameters at different ages (Table 4, Fig. S4). At every age, the first discriminant factor of the DFA was mainly correlated with frequency parameters: the fundamental frequency of the 1st voice (F01CC) and the 25% quartile (Q25CC).

For SCs, although the DFAs were based only on 3 acoustic parameters, the classification rates approximated 80% (Table 5). The first functions, which explained 52.9–78.3% of the total variance, were strongly correlated with MF0SC at each age (Table 5).

Table 2. Mean, SD and potential individual coding (PIC) values of acoustic parameters of the contact call of North African houbara bustard chicks (abbreviations and definitions of parameters are provided in Table 1)

Acoustic parameters	Age	Mean	SD	PIC
DSCC (s)	1	0.384	0.129	2.426
	2	0.437	0.126	1.998
	3	0.466	0.119	1.948
	4	0.461	0.143	1.528
NUCC	1	4.473	1.235	2.228
	2	6.233	1.898	2.363
	3	7.738	2.122	2.189
	4	7.667	2.686	1.925
TCC	1	12.19	2.234	3.656
	2	14.26	1.792	2.618
	3	16.58	1.746	2.647
	4	16.57	2.454	2.824
DUCC (s)	1	0.053	0.011	2.451
	2	0.046	0.009	1.8
	3	0.04	0.007	1.435
	4	0.037	0.01	1.481
DIUCC (s)	1	0.04	0.02	1.893
	2	0.027	0.016	1.569
	3	0.016	0.014	1.149
	4	0.021	0.013	1.267
F01CC (Hz)	1	1689	127.9	2.109
	2	1450.4	177.1	3.039
	3	1184.1	152.2	4.13
	4	1081.1	131.7	4.323
F02CC (Hz)	1	1838.9	148.5	2.687
	2	1508.8	204.8	2.408
	3	1219	153.1	4.225
	4	1099.2	124.7	3.91
GCC (Hz)	1	15.17	38.82	4.34
	2	58.37	96.71	1.811
	3	34.78	60.77	6.702
	4	18.09	47.58	10.678
Q25CC	1	1782.6	152.6	1.725
	2	1464	178.3	1.949
	3	1218.4	154.8	2.658
	4	1098.8	119.4	2.833
Q50CC	1	1839.1	160.9	1.678
	2	1508.9	183.3	1.907
	3	1272.7	162.5	2.079
	4	1149.6	140.8	1.866
Q75CC	1	1898.8	217.2	1.551
	2	1701.7	581.6	1.458
	3	1743.2	781.4	1.812
	4	1868.5	1150.8	1.761
E1500CC	1	0.051	0.057	1.444
	2	0.458	0.349	0.853
	3	0.732	0.204	1.664
	4	0.759	0.11	1.459

For both call types, the classification rate (percentage of calls correctly classified) changed with age. For CCs, the classification rate decreased from 95.3% at Age 1 to 84% at Age 4 (Table 4). In contrast,

Table 3. Mean, SD and potential individual coding (PIC) values of acoustic parameters of the distress call of North African houbara bustard chicks (abbreviations and definitions of parameters are provided in Table 1)

Acoustic parameters	Age	Mean	SD	PIC
DSC (s)	1	0.374	0.061	2.514
	2	0.379	0.078	2.831
	3	0.455	0.091	2.874
	4	0.483	0.09	2.711
F01SC (Hz)	1	2028.8	187.7	2.756
	2	1598.7	128.2	2.829
	3	1378.3	142.5	3.635
	4	1177.9	137.5	4.557
F02SC (Hz)	1	NA	NA	NA
	2	1653.3	143.2	3.354
	3	1441.2	180.8	4.134
	4	1218.5	146.1	4.833
MF0SC (Hz)	1	1946.9	156.9	3.864
	2	1572.7	136.8	3.528
	3	1331	151.9	4.708
	4	1145.3	134.2	4.571
GSC (Hz)	1	0	0	0
	2	54.55	69.94	8.691
	3	62.81	81.58	11.11
	4	40.54	37.2	4.492

for SCs, the classification rate slightly increased with age in relation to the significant loading effect of GSC on the second or third discriminant function (Table 5). Indeed, the 2-voice phenomenon appeared in the SCs after Age 1 (Table S1).

3.2. Weight effect on acoustic parameters

In order to test for a potential effect of weight on the acoustic parameters of the 2 types of vocalisations, wherein weight can vary from one individual to another (range: Age 1: 30–47 g; Age 2: 127–213 g; Age 3: 260–439 g; Age 4: 320–570 g), we performed a series of GLMMs. For CCs, models showed that weight is a poor predictor of the acoustic parameters with the exception of duration of the entire sequence (DSCC) and tempo (TCC) at Age 1, TCC at Age 3, F01CC at Age 4 and Q25CC at Age 4 (Table S2). All repeatability estimates were highly significant ($p < 0.0001$), with DSCC ($R_{adj} = 0.789$, 95% CI = 0.567–0.888 vs. non-adjusted $R = 0.877$, 95% CI = 0.737–0.935) and TCC ($R_{adj} = 0.865$, 95% CI = 0.695–0.931 vs. non-adjusted $R = 0.892$, 95% CI = 0.659–0.914) at Age 1, TCC ($R_{adj} = 0.709$, 95% CI = 0.412–0.836 vs. non-adjusted $R = 0.846$, 95% CI = 0.656–0.922) at Age 3 and F01CC ($R_{adj} = 0.903$, 95% CI = 0.77–0.95 vs. non-adjusted $R = 0.922$, 95% CI = 0.823–0.959)

Table 4. First 3 discriminant functions (DF1, DF2, DF3) of the DFA performed with 7 acoustic parameters of the contact call of the North African houbara bustard chick. PVE: proportion of variance explained; RD: discrimination rate; CV: cross-validation. Variables that contributed most to DF1, DF2 and DF3 are in **bold** (abbreviations and definitions of parameters are provided in Table 1)

	Age 1			Age 2			Age 3			Age 4		
	DF1	DF2	DF3	DF1	DF2	DF3	DF1	DF2	DF3	DF1	DF2	DF3
DSCC	-0.208	0.366	0.159	0.223	0.228	0.716	-0.154	0.250	-0.269	0.094	-0.172	0.128
TCC	0.359	-0.869	-0.221	0.184	0.640	-0.654	0.211	0.683	-0.146	0.041	-0.709	-0.309
DUCC	-0.213	0.253	-0.590	0.180	-0.294	-0.180	-0.042	0.049	0.016	0.095	0.269	0.054
F01CC	0.547	0.497	-0.547	-0.573	0.284	-0.158	0.747	-0.488	-0.180	-0.609	0.163	-0.614
GCC	0.219	0.091	0.594	0.010	0.103	-0.604	0.064	0.472	0.846	0.671	-0.016	-0.716
Q25CC	0.716	0.548	-0.357	-0.603	0.333	-0.264	0.783	-0.494	-0.096	-0.632	0.149	-0.677
Q50CC	0.668	0.515	-0.309	-0.621	0.367	-0.317	0.474	-0.177	0.147	-0.244	0.009	-0.313
PVE	0.438	0.249	0.13	0.664	0.183	0.068	0.608	0.231	0.109	0.476	0.279	0.215
RD (%)		95.333			90			88.461			84	
CV (%)		92.667			84.667			76.154			69.333	

Table 5. First 2 or 3 discriminant functions (DF1, DF2, DF3) of DFA analysis performed with 3 acoustic parameters of the distress call of the North African houbara bustard chick. PVE: proportion of variance explained; RD: discrimination rate; CV: cross-validation. Variables that contributed most to DF1, DF2 and DF3 are in **bold** (abbreviations and definitions of parameters are provided in Table 1). Note that for Age 1, the first 2 discriminant functions explained 100% of the total variance

	Age 1		Age 2			Age 3			Age 4		
	DF1	DF2	DF1	DF2	DF3	DF1	DF2	DF3	DF1	DF2	DF3
DSC	-0.293	0.956	0.459	0.587	-0.667	-0.350	0.081	0.933	0.393	0.156	0.907
MF0SC	0.999	0.044	-0.803	0.532	0.269	0.971	-0.227	0.071	0.935	-0.236	0.264
GSC	NA	NA	-0.307	-0.410	-0.859	0.384	0.918	-0.094	0.195	0.969	-0.154
PVE	0.783	0.218	0.530	0.285	0.185	0.529	0.343	0.128	0.67	0.237	0.092
RD (%)		68.667		80			80.667			81.429	
CV (%)		62.667		75.333			76			75	

and Q25CC ($R_{adj} = 0.913$, 95% CI = 0.785–0.952 vs. non-adjusted $R = 0.93$, 95% CI = 0.837–0.963) at Age 4 exhibiting high individual repeatability.

In SCs, neither call duration (DSC) nor GSC were significantly influenced by chick weight at any age (Table S3). However, weight was a significant predictor of fundamental frequency of the 1st voice (F01SC) at Age 4 only. Adjusted repeatability remained high and comparable to the non-adjusted value ($R_{adj} = 0.927$, 95% CI = 0.818–0.963 vs. non-adjusted $R = 0.943$, 95% CI = 0.863–0.971).

3.3. Age effect on acoustic parameters

Except for GCC, chick age was important in predicting all acoustic parameters of both call types including the fundamental frequency, which significantly decreased with age (Tables S4 & S5, Figs. 3 & 4). For all models, the inclusion of heteroscedastic and autocorrelation functions improved the fit by considerably decreasing Akaike's information criterion (AIC) scores compared to the models without

variance and residual autocorrelation functions. Hence, these complex models provided more accurate inference.

Overall, we found that the repeatability over time of the acoustic parameters measured for both call types was high (range: 0.35–0.77; Tables S6 & S7), suggesting that acoustic individuality is preserved over time. In agreement with this result, the correlation plots also showed a strong relationship among the average acoustic parameter measures per chick recorded at different ages (Figs. S5 & S6).

4. DISCUSSION

Parent-offspring recognition is mutually beneficial: chick fitness and adult reproductive success may depend on the ability of offspring to emit individualised signals and parents to perceive individuality within those signals (Trivers 1974). In this study, we found that several acoustic parameters are individualised in both CCs and SCs produced by houbara chicks. Indeed, for all measured acoustic para-

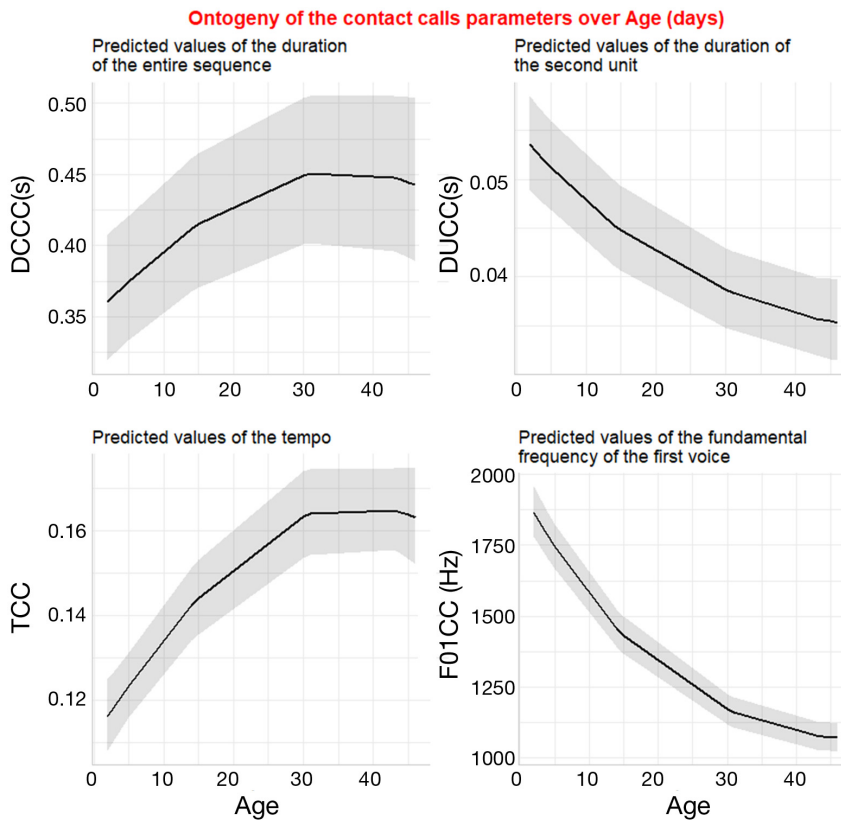


Fig. 3. Mixed regression models showing the effect of age on contact call parameters of North African houbara bustard chicks; see Table 1 for acronym definitions. Each panel shows the fitted regression line and the 95% confidence interval band

parameters (except E1500CC at Age 2 and GSC at Age 1), the mean intra-individual CV was lower than the inter-individual CV, and for several parameters the PIC, exceeding a value of 2, showed a high probability for individual coding (Scherrer 1984). Similarly, DFA showed that the potential individual identity coding is multiparametric and relies mainly on spectral parameters. Therefore, our results show that CCs and SCs remain individualised throughout chick development and may thus allow for the vocal recognition of chicks by their mothers at all ages. Although this study focused on male chicks, we expect similar results in female chicks; additional vocal recordings and analyses should be carried out on female chicks to test this prediction.

In CCs, we observed a slow decline in overall classification rates, which decreased more than 10% from the first to the fourth age class of recordings (an age span of approximately 6 wk). The finding that between-individual differences in call structure are the most extreme in the first days of life supports the prediction that such differences function to maximise reliable recognition of chicks by mothers at a life

stage when individual recognition is critical for their survival. Time-specific development of individuality cues has been observed in several other bird species, although mainly in colonial or group-living birds. For example, in cranes, the highest expression of individuality occurred during the period when chicks left their sedentary family life for a gregarious life in dense migratory flocks (Goncharova et al. 2015). Similarly, in bank swallows *Riparia riparia*, thick-billed guillemots *Uria lomvia*, jackass penguins *Spheniscus demersus*, razorbills *Alca torda* and pinyon jays *Gymnorhinus cyanocephalus*, vocal parent–young recognition is achieved by the time the young leave the nest to form stable crèches of dependent young (Beecher 1981, 1991, McArthur 1982, Seddon & Van Heezik 1993, Lefevre et al. 1998, Insley et al. 2003). For the houbara, in the first days after hatching, chicks are completely dependent on their mother for thermoregulation and food (beak-to-beak feeding of mainly invertebrate prey; Bourass 2012), which may explain higher discrimination rates (95%) observed at the early ages.

After that age, chicks learn to peck grass and small invertebrates and gradually acquire feeding autonomy (Collar 1996). The decrease in discrimination rates—and so the erosion of vocal individuality across the ages—occurs in parallel with their gradual autonomy in search of food.

The discrimination rates of the SCs did not decrease with age. On the contrary, classification rates for these calls increased with age, from 68% at Age 1 to $\geq 80\%$ at other ages. This is mainly linked to the emergence of the 2-voice phenomenon after Age 1. Similar patterns have been observed in 3 crane species: the demoiselle crane *Anthropoides virgo*, the red-crowned crane *Grus japonensis* and the Siberian cranes *G. leucogeranus* (Goncharova et al. 2015). In these species, nonlinear phenomena (irregular oscillations of sound-producing membranes) in calls significantly increased with age, thereby increasing the potential for individual recognition. Here, 2-voice production increased call diversity and hence the potential for individual coding of SCs. Contrary to the gradual autonomy in search of food across ages, houbara chicks remain fully dependent on maternal

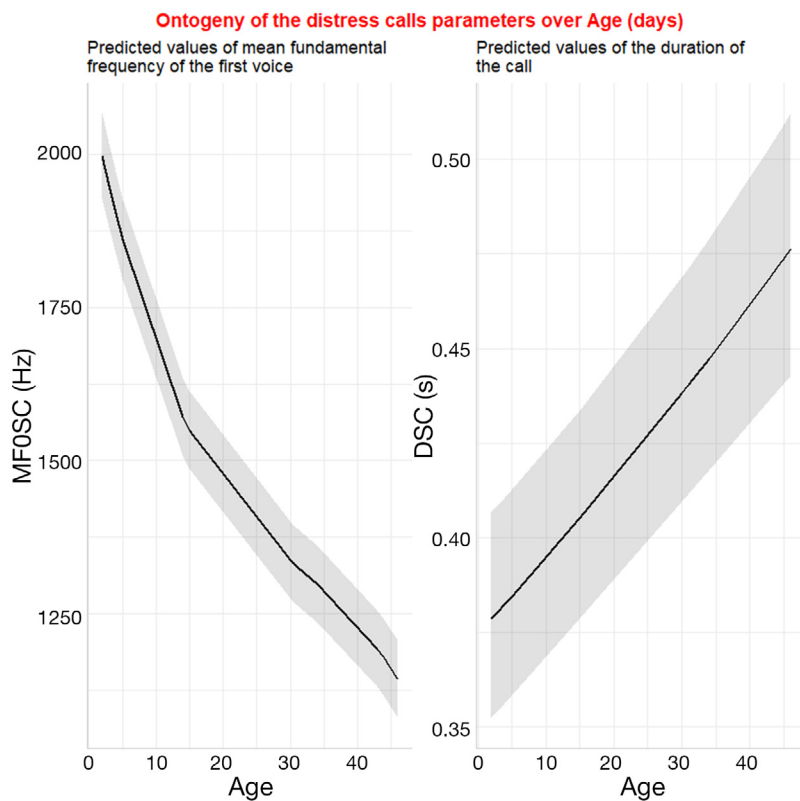


Fig. 4. Mixed regression models showing the effect of age on distress call parameters of North African houbara bustard chicks; see Table 1 for acronym definitions. Each panel shows the fitted regression line and the 95% confidence interval band

care for protection against predators prior to fledging (around 60 d after hatching). Furthermore, during the fledgling period, while chicks become more independent in their search for food, their exploratory and foraging movements tend to increase, increasing the distances separating them from their mother or siblings. In case of danger (e.g. presence of a fox, flying raptor), the female will produce an alarm call and all chicks will freeze, lying down on the ground or under a bush, remaining silent and relying on the concealment provided by their plumage. Once the predator is gone, the female will call for her chicks, waiting for response to reunify the entire brood and move to a safe location (C. Cornec pers. obs.). Under such conditions, accurately identifiable SCs might help the female to quickly locate all her chicks, a trait potentially under high selective pressure based on the low productivity observed in the species (0.48 ± 0.26 fledglings per female) mainly due to high predation rates on clutches and broods (see Bacon 2017).

Although a relationship between body weight and call acoustic parameters (notably the frequency parameters) has been previously reported for several bird

species (Appleby & Redpath 1997, Hardouin et al. 2007, Mager et al. 2007, Miyazaki & Waas 2003, Abdel-Kafy et al. 2020), including adult houbara males (Cornec et al. 2015), we show here that chick weight largely remains a poor proxy of acoustic parameters in CCs and SCs within age groups among houbara chicks. Moreover, based on adjusted and non-adjusted repeatabilities, the individual signature found in houbara chicks does not appear to be linked to differences in weight across individuals.

On the other hand, longitudinal recordings revealed that acoustic parameters of CCs and SCs produced by chicks varied with age, wherein vocalizations became lower-pitched with time. These results are similar to those reported in some other precocial species, where a decline in frequency was observed across the chicks' vocal development (Adret 2012). In non-vocal learning species, changes in the acoustic structure of vocalizations during ontogeny are closely related to the maturation processes (the sound-producing morphological structures, changes in hormone levels and the

maturation of the sensory mechanism linked to vocal organs), and to some extent in some species to maternal presence and emotional state during development, and are largely genetically determined (Konishi 1963, Lade & Thorpe 1964, Konishi & Nottebohm 1969, Kroodsmas & Miller 1996, Desmedt et al. 2020). During maturation of vocal organs (e.g. ossification of trachea and bronchi, size and elasticity of the trachea, size of the tympaniform membranes), some anatomical structures develop gradually into adult form and shape whereas others follow an abrupt transformation related to 'the breaking of the voice' as in collared doves *Streptopelia decaoct* (Ballintijn et al. 1995). Similarly, in houbara chicks, changes in frequency parameters with age in CCs and SCs may result from maturation of the vocal structure, i.e. variation in tracheal and syrinx size (Fitch & Hauser 2003). In the same way, changes observed in temporal parameters could be due to an increase in lung capacity or air sac volume (in birds) throughout chick development/growth (Fitch & Hauser 2003). Finally, we showed that some acoustic parameters stabilise after Age 3.

Despite the well-individualized acoustic parameters found in houbara chicks, changes in these acoustic parameters with age may nevertheless affect parental recognition mechanisms. Reliable individual recognition is based on individually distinctive cues which must not be condition-dependent, not be associated with fitness differences and must be fixed and stable across time (Dale et al. 2001). But as shown in several species of seals, an evolution of the call's parameters during ontogeny does not rule out the possibility of efficient mother–offspring vocal recognition (Insley 2000, Charrier et al. 2003, Sauvé et al. 2015a,b). Long-term recognition requires flexible learning and memory, whereby parents need to constantly adjust the template of their offspring's call (Hepper 1991). The mother houbara and her chicks remain in contact throughout the rearing period (about 8 wk). Mothers must continuously learn their chick's changing voice, taking into account age-related effects on calls. This learning process could be facilitated by the fact that the acoustic parameters coding individuality remain relatively the same in the first 6 wk of the houbara chick's life. This should allow mothers to learn only a single, stable set of acoustic variables to maintain vocal recognition as chicks grow. High adjusted repeatability computed on global models along with the correlation plots supports these findings, suggesting a potential consistency of the individual signature across age. However, these possibilities remain hypothetical and need to be tested with playback experiments performed at different chick ages.

To conclude, this study has demonstrated that CCs and SCs produced by male houbara chicks convey identity information throughout their development. The individual recognition processes maintaining parent–young bonds remain unknown in this species and need to be addressed in future playback experiments testing maternal recognition of offspring throughout the offspring's development. We also observed developmental changes in the temporal and spectral structure of CCs and SCs related to age. Further anatomical and physiological investigations may reveal which organ parts are involved in these changes during houbara ontogeny.

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