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The vocal development of the Red-crowned Crane *Grus japonensis*

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Abstract Most studies on avian vocal ontogenesis have focused on taxa exhibiting some kind of vocal learning. This study provides a detailed analysis of vocal processes through early and late ontogenesis in 17 chicks of the Red crowned Crane *Grus japonensis*, a species lacking vocal learning. Three basic structural classes: trills, PE-chirps and PS-chirps and their transitional forms are described. Trends in call parameter values are presented for 10 age classes in the course of a period from birth to 9.5 months. We discuss our vocal classification with those reported for other crane species, relate the revealed stages of vocal ontogenesis in the Red-crowned Crane to biologically relevant life stages in this species and advance a hypothesis for the proposed function of retaining high juvenile frequencies in adolescent cranes for a prolonged period, up to voice breaking (a rapid significant decrease in fundamental frequency). We conclude, that voice breaking is universal for both sexes and that the retained high call frequencies may represent an infantile characteristic, essential in evoking care from the parents towards the growing chick and may also act as a mechanism to reduce aggression from conspecifics.

Key words Call, Gruidae, Non-passerine, Ontogenesis, Vocalization, Voice breaking

The formation of definitive adult vocal repertoires in birds through ontogenesis has a long research history, however, most studies have been devoted to species, exhibiting some kind of vocal learning, either passerines (e.g., Kroodsmas & Baylis 1982; Marler & Peters 1982; Catchpole & Slater 1995), or non-passerines, e.g. parrots (Britten-Powell et al. 1997; Bond & Diamond 2005); or hummingbirds (Jarvis et al. 2000). Such biases towards species with vocal learning are probably a function of interest in drawing analogies between learned avian vocalization and human speech, which is also acquired through learning (Fitch 2000; Jarvis 2004). Nevertheless, data from bird species that lack vocal learning are important in allowing comparisons of different communication systems (similar to comparisons between verbal and nonverbal communication in mammals).

Furthermore, non-passerines that do not exhibit vocal learning provide an avian model for studying

voice breaking—a rapid, significant decrease in fundamental frequency from high juvenile frequencies to low adult frequencies taking place over a few days or weeks (Abs 1980; Radford 2004). The developmental traits diagnostic of this phenomenon are thought to have been favoured by various selection pressures, the mechanisms involved are probably not uniform between species. In humans, adolescent voice breaking is male-specific and due to sexual selection (Fitch & Giedd 1999; Fitch 2000). In contrast in various species of birds, chicks may develop adult voices either through a steady decrease in vocal frequency (as is the case in the human female or among geese (Würdinger 1970; ten Thoren & Bergmann 1986, 1987), or through voice breaking, as in human males, in Leach's Storm-Petrel *Oceanodroma leucorhoa* (Taoka et al. 1989; Naugler & Smith 1992) and in various cranes (Archibald 1976), or by a combination of the two, exactly as in humans with sex-specific vocal ontogenesis, such as for example the Green Woodhoopoe *Phoeniculus purpureus* in which males exhibit voice breaking, and females do not (Radford

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2004). Selection pressures favoring voice breaking amongst birds have not previously been studied.

Cranes represent an interesting model for studying vocal development in non-passerines. There is no evidence in the literature of any vocal learning in this avian group. Voice breaking has not yet been studied in detail in cranes, and different authors have used different terms for this stage of vocal development. For the genus *Grus*, voice breaking from the high juvenile frequency to the low adult frequency was reported at the age of 10–11 months (Archibald 1976; Niemeier 1979; Nesbitt & Bradley 1996), for one individual Eurasian Crane *Grus grus* it was reported to have occurred at an age of nine months (Gebauer & Kaiser 1998) and for one individual Siberian Crane *G. leucogeranus* it occurred as early as at five or six months of age (Bragina 2005). For the Sandhill Crane *G. canadensis* and for the Grey Crowned Crane *Balearica regulorum*, juvenile high frequency vocalizations have been reported as being retained to up to nine or ten months of age (Niemeier 1979; Budde 1999, 2001).

Data on vocal development in cranes are scarce. The available classifications for the chick call types of four Gruinae species (Archibald 1976; Nesbitt & Bradley 1996), took into account the contexts of call production rather than call structure. Only in the case of the Sandhill Crane have calls been classified on the basis of structure, with Niemeier (1979) providing descriptions of two types of chick calls: trills and chirps. The Red-crowned Crane *G. japonensis* is a good model species for studying the developmental traits of voice breaking, since only for this species have the various influences of factors such as individuality, sex and kin, on call variability throughout ontogenesis been studied (Klenova et al. 2004, 2005, in press). In particular, previous studies have revealed that the influence of individuality on vocal variability is much stronger, than that of either gender or kin (Klenova et al. 2004, 2005, in press). These facts justify the study of the vocal changes taking place in individuals of both sexes before voice breaking in this species.

The Red-crowned Crane is one of the rarest crane species, with a wild population of only about 2,100 birds (Archibald 2003). Both of the parents invest together to raise one or sometimes two chicks, which leave the nest soon after hatching (Masatomi 1981; Vinitser 1981). The parent-chick social bond is maintained for up to eight or nine months, and is broken only during late winter on the wintering grounds

prior to the parents commencing a new breeding season (Kamata 1994). Thus, a period of vocal ontogenesis occurs during the following life phases of the chicks: following the parents on foot through a large family territory, flight acquisition, formation of pre-migratory flocks, autumn migration and wintering. Throughout this period the chicks are under parental care and protection (Masatomi 1981; Vinitser 1981; Kamata 1994).

By the age of 90 or so days Red-crowned Crane chicks, like other crane chicks, complete tracheal elongation, i.e., the formation of the peculiarly complex tracheal loops inside the sternum (Rüppell 1933; Niemeier 1979; Gaunt et al. 1987; Fitch 1999). By the age of 110 days, the chick will have almost completed its growth phase and reaches an average body mass of 7.32 kg (compared to just 0.15 kg on hatching; Postelnykh & Kashentseva 2005). Evidence available for other crane species (Archibald 1976; Niemeier 1979; Nesbitt & Bradley 1996; Gebauer & Kaiser 1998; Budde 1999, 2001) suggests that voice breaking is not correlated with the completion of body growth or vocal apparatus growth, but is postponed to an age of eight to ten months, i.e., when the young cranes begin their independent life.

In this study, we expected to find that, like other crane species, Red-crowned Crane chicks retain high juvenile vocal frequencies for a prolonged period until voice breaking. We also expected to find some gradual changes in juvenile voice, resulting from a combination of body growth and the development of new activities, such as flying. Interactions between the two processes—of retaining high juvenile frequencies, and of gradual changes in the voices of growing chicks—remain poorly understood, and the function of retaining high vocal frequencies in cranes is unclear. In studying the vocal ontogenesis of this species in detail, our purpose was to describe explicitly the vocal traits leading to voice breaking in the Red-crowned Crane.

MATERIALS AND METHODS

1) Study sites and subjects

Our subjects were 17 Red-crowned Crane chicks studied from hatching to 9.5 month of age. Five males and nine females (Nos 1 to 14) were kept in the Oka Crane Breeding Centre of Oka Biosphere State Nature Reserve (Ryazan region, Russia), two females (Nos 15 and 17) were kept in Moscow Zoo (Russia) and one female (No. 16) was kept in Tierpark-Berlin

(Germany). Fourteen chicks were raised by their genetic or conspecific adoptive parents in green enclosures about 100 m² per family; and three chicks (Nos 2, 11 & 13) were human-raised. The chicks hatched from 18 May to 11 July 2003 and from 11 May to 9 June 2004. The parent-raised chicks were separated from their parents at the age of three or four months in the Oka Crane Breeding Centre and Tierpark-Berlin; and at the age of nine or ten months, before

the beginning of the new breeding season in Moscow Zoo. After separation, the chicks were kept in groups of 3–8 individuals. The chicks were sexed using DNA PCR-amplification (Griffiths et al. 1998) independently by two laboratories.

2) Call recordings

We recorded the calls of the chicks in summer, autumn and winter 2003–2004, in the morning or in the

Table 1. Call samples taken from individual Red-crowned Crane chicks: a—for the analysis of calls belonging to each of four structural classes (PE-chirps, PS-chirps, trills and transitional chirp-to-trill calls); b—for the analysis of age-related shifts in the structure of trills; c—for the analysis of age-related shifts in the structure of PE-chirps.

Chick	Analysis	Age class (days)									
		Age 1 0–4	Age 2 5–14	Age 3 15–24	Age 4 25–34	Age 5 35–44	Age 6 45–54	Age 7 55–84	Age 8 85–144	Age 9 145–204	Age 10 205–284
Female 1	a	200	172	200	200	200					
	b/c	0/0	0/0	0/0	0/0	0/0					
Female 2	a	200	200	200	200	200	200	200	200		
	b/c	20/0	20/0	20/0	20/0	20/0	20/0	20/0	20/0		
Male 3	a	200	200	200	133	165	200	155	200	200	
	b/c	20/20	20/20	20/20	20/13	20/20	20/20	20/20	20/20	2/20	
Male 4	a	200	135	200	200	200		149	200		
	b/c	0/0	0/0	0/0	0/0	0/0		0/0	0/0		
Female 5	a	200	200	200	200	200		200	200	200	
	b/c	20/0	20/0	20/0	20/0	20/0		20/0	20/0	8/0	
Male 6	a	200	162	200	200			0	200	200	
	b/c	15/0	20/0	20/0	20/0			20/0	20/0	20/0	
Female 7	a		200	150	200	200	200	200	200	200	
	b/c		0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0	
Female 8	a		200	160	200	200	200	200	200	155	
	b/c		0/20	0/5	0/20	0/20	0/20	0/20	0/20	0/3	
Male 9	a	200	200	200	200	200	200	200	200	200	200
	b/c	20/20	20/20	20/20	20/20	20/20	20/20	20/20	4/20	20/20	0/0
Female 10	a	200	200	200	200	200	200	200	200	200	155
	b/c	0/20	0/20	0/9	0/14	0/20	0/20	0/20	0/20	0/20	0/0
Female 11	a	200	200	200	184	200	200	200	200	200	200
	b/c	20/20	20/20	20/20	8/20	20/20	20/20	20/20	20/20	20/20	0/0
Male 12	a	200	200	200	179	178	200	170	0	156	
	b/c	20/20	20/20	20/20	20/20	20/20	13/16	9/15	0/12	20/0	
Female 13	a	200	200	200	200	200	200		200	200	175
	b/c	20/20	20/20	20/20	20/20	20/20	0/20		20/20	15/20	0/0
Female 14	a	200	200	200	200	200	200		200		
	b/c	0/0	0/0	0/0	0/0	0/0	0/0		0/0		
Female 15	a	200								200	
	b/c	0/0								0/0	
Female 16	a								176		
	b/c								0/0		
Female 17	a		200						200	200	200
	b/c		0/0						0/0	0/0	0/0
Total	a	2600	2869	2710	2696	2543	2000	1874	2776	2311	930
	b/c	155/120	160/140	160/114	148/127	140/140	93/136	129/115	124/132	105/103	0/0

evening, during periods of high activity for the chicks. Each recording session lasted 45–60 minutes. The distance to birds varied from 1.5 to 15 m. In the Oka Crane Breeding Centre, calls were recorded once every 5–7 days from hatching to 1.5–2.5 months of age and thereafter once every two months. In Moscow Zoo, calls were recorded once every two months. We used a Marantz PMD-222 cassette recorder (D&M Professional, Kanagawa, Japan) with a shotgun condenser Sennheizer K6-ME67 microphone (Sennheizer electronic, Wedemark, Germany).

3) Age classes

Since the hatching dates differed between chicks, we classified all recorded calls into ten age classes, hereafter referred to as “Ages” (Table 1). The boundaries between the ten Ages were drawn according to four biologically relevant life stages of a chick. During the first stage (Age 1) chicks were relatively sluggish and stayed close to their nest; during the second stage (Ages 2–7) chicks actively followed their parents; during the third stage (Ages 8 & 9) chicks completed the rapid phase of growth (Postelnykh & Kashentseva 2005) and became capable of flight. In the wild, the third stage coincides with the period of the autumn migration. The fourth stage (Age10) covers the winter, and ends, in the wild, with the disruption of the parent-chick family bond.

4) Call measurements

Both digitizing (22.05 kHz sampling rate, 16 bit precision) and call measurements were made with Avisoft-SASLab Pro v. 4.3 (© R. Specht). Spectrograms were created with Hamming window, FFT-length 512 points, frame 50% and overlap 93.75%, providing time resolution of 1.5 ms and frequency resolution of 43 Hz.

The calls were classified visually based on their screen spectrograms into structural types. For all call types, we measured the maximum fundamental frequency (F_{max}) and the total duration of each call (Dur_{total}) (Fig. 1). For pulsed calls, we also measured the minimum fundamental frequency (F_{min}) and the mean pulse period (Period). We calculated the Period in the following way: we divided the total duration of 5–12 successive pulses, measured as the duration from the fundamental frequency maximum point of a preceding pulse to the fundamental frequency maximum point of a following pulse, by number of measured pulses (Fig. 1a).

For non-pulse calls, we also measured the initial

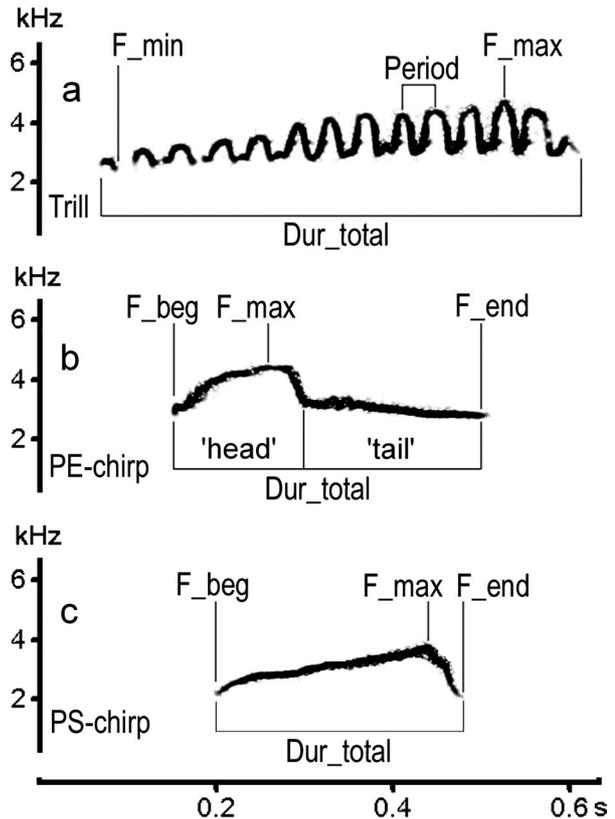


Fig. 1. Parameter measurements taken from trills (a), PE-chirps (b) and PS-chirps (c) of Red-crowned Crane chicks: F_{min} —minimum fundamental frequency; F_{max} —maximum fundamental frequency; F_{beg} —initial fundamental frequency; F_{end} —final fundamental frequency; Dur_{total} —total duration of a call; “head”—duration from beginning a call to a point of inflection in a frequency contour; “tail”—duration from a point of inflection to the end of a call; Period—duration of one pulse.

fundamental frequency (F_{beg}), the final fundamental frequency (F_{end}), the duration from the beginning of a call to the point of maximum fundamental frequency ($Dur_{beg-max}$), the duration from the point of maximum fundamental frequency to the end of the call ($Dur_{max-end}$). For non-pulse calls, we selected F_{min} as a minimum value among the F_{beg} and F_{end} (Fig. 1b, c). For some non-pulse calls, we additionally measured the duration from the beginning of a call to a point of inflection in a frequency contour (“head”) and the duration from the point of inflection to the end of a call (“tail”).

For all calls, we calculated the depth of frequency modulation dF as the difference between the maximum and minimum fundamental frequencies.

For calls with two independent fundamental fre-

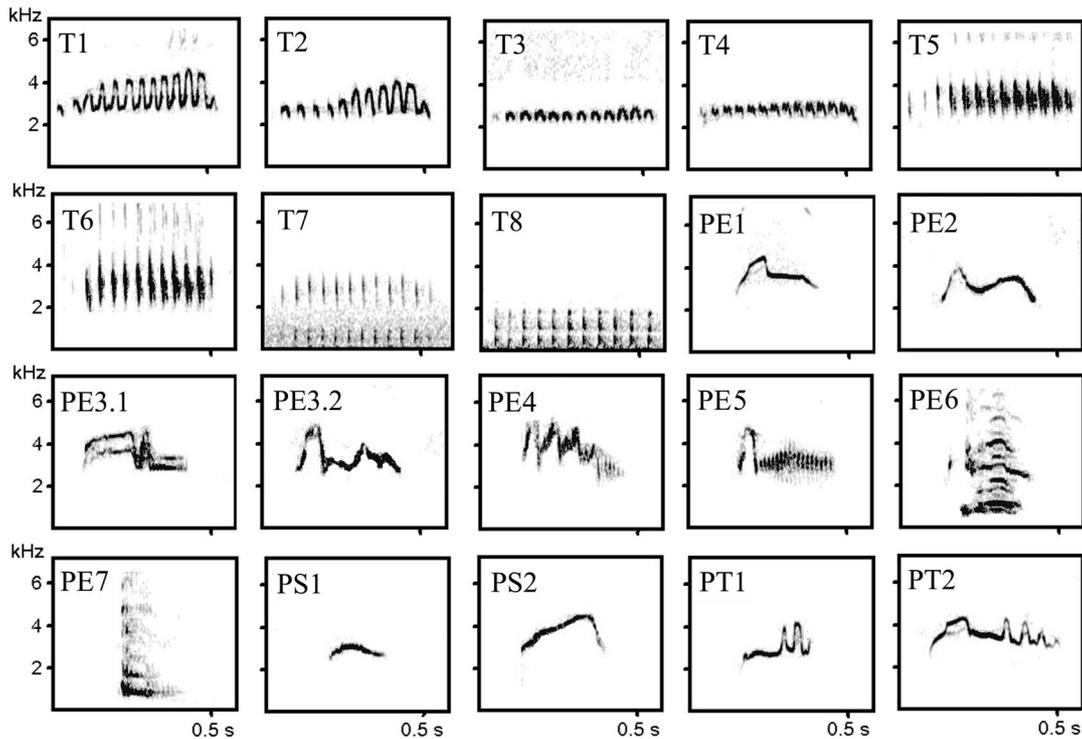


Fig. 2. Call structures occurring throughout the vocal ontogenesis of the Red-crowned Crane, from hatching to 10 months of age. T1–T6—trills, T7—voice breaking trill of an adolescent female, with two independent frequency components—the retained high juvenile frequency and the newly appearing low adult frequency; T8—the definitive adult trill, derived from the chick trill after voice breaking; PE1–PE5—PE-chirps; PE6, the chirp of an adolescent female while voice breaking, with two independent frequency components—the retained high juvenile frequency and the newly appearing low adult frequency; PE7 - adolescent adult-like calls, derived from a chick chirp, but already lacking the high juvenile frequency component. PS1–PS2—PS-chirps; PT1–PT2—transitional chirp-to-trill calls.

quencies occurring in a spectrum (e.g., Fig. 2, PE3.1), we measured the upper of these frequency bands.

5) Statistics

We used the non-parametric Mann-Whitney U-test for comparison of samples and non-parametric Spearman rank correlation test to calculate correlations in call parameter values with Ages. All statistical analyses were made in STATISTICA, version 6.0 (StatSoft, Inc, Tulsa, OK, USA). The averages are given as mean ± SD.

RESULTS

1) Call types

At any Age we could clearly recognize two different call structures: pulse “trills” and non-pulse “chirps” (Fig. 3a, b). “Chirps” were further split into two classes based on the contours of frequency modulation: simple humped PS-chirps (peak-simple chirps) and the PE-chirps (peak-and-extension

chirps), with one or more additional inflections (Fig. 1b, c, 2, 3c). Overall, we subdivided calls into four structural classes: trills, PS-chirps, PE-chirps, and transitional chirp-to-trill calls.

Trills

Trills were tonal pulse calls, with either continuous or broken trace of frequency modulation (Fig. 1a). Trills occurred in peaceful parent-chick and food contexts, and never in dangerous or stressful contexts. We split the trills into seven types T1–T7 based on pulse shapes and the number of breaks between the pulses, and assigned the abbreviation T8 to the corresponding trill-derived adult call (Fig. 2, T1–T8): T1—continuous contour, bell-shaped pulses; T2—as T1, but with two or more silent intervals; T3—as T1, but all pulses are broken with silent intervals; T4—as T3, but with at least two pulses W-shaped; T5—as T4, but two or more pulses are stroke-shaped; T6—as T5, but all pulses are stroke-shaped or double-stroke-shaped; T7—trill with breaking voice (All, or some,

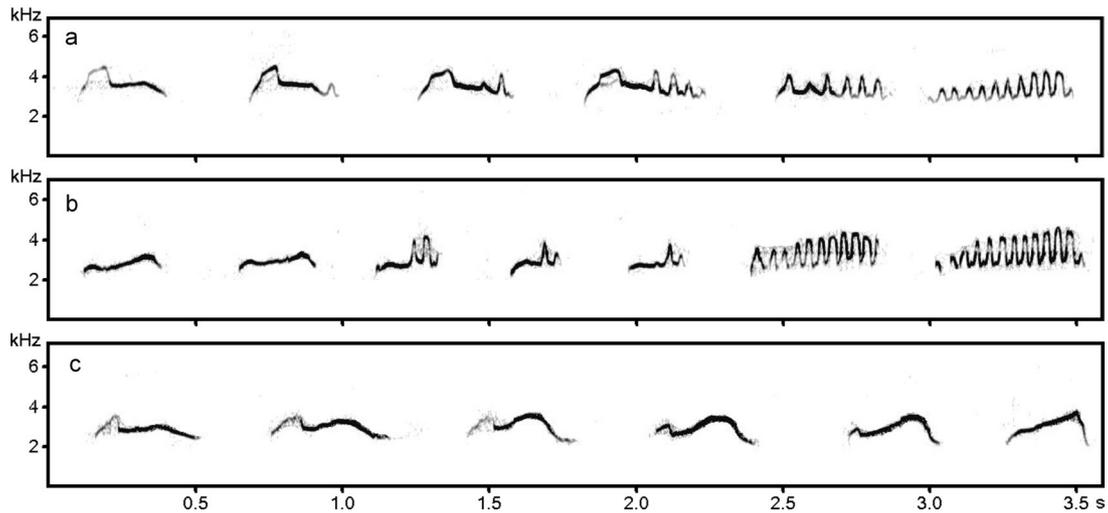


Fig. 3. Gradual changes in Red-crowned Crane chick call structures: (a) transitions from PE-chirp to trill; (b) from PS-chirp to trill; (c) from PE-chirp to PS-chirp. The three sequences were taken from three individuals.

pulses have the low-frequency (adult-like) component below 1.5 kHz); T8—the definitive adult pulse call, from which the high-frequency juvenile component is lacking. The MPP was 43 ± 3 ms, Dur_{total} 467 ± 97 ms, F_{max} 3.58 ± 0.55 kHz, dF 1.27 ± 0.47 kHz. (N=13 chicks of Ages 1–9; 5 males, 7 females, N=1774 calls, from 60 to 188 calls per chick).

PS-chirps

PS-chirps, one-humped tonal calls (Fig. 1c), were given in food or parent-following contexts, but more often during dangerous or stressful situations (capture, cooling etc.). PS-chirps were split into two types based on the position of the F_{max} point: PS1, with the F_{max} point at the beginning or in the middle of the call and PS2 with the F_{max} point at the end of the call (Fig. 2, PS1–PS2). For PS2-type chirps, the Dur_{total} was 211 ± 64 ms, Dur_{beg-max} 164 ± 57 ms, Dur_{max-end} 47 ± 17 ms. The F_{beg} was 2.52 ± 0.23 kHz, F_{end} 2.55 ± 0.24 kHz, F_{max} 3.25 ± 0.40 kHz, dF 0.81 ± 0.34 kHz. (N=6 chicks of Ages 1–4; 3 males, 3 females, N=611 calls, from 78 to 133 calls per chick).

PE-chirps

PE-chirps, non-pulse tonal calls with a humped ‘head’ coming through inflection into the smoothly lowering ‘tail’ (Fig. 1b), were given during contexts such as parent-chick contact, flight acquisition, food and disturbance. PE-chirps were split into seven types based on the frequency modulation contour

(Fig. 2, PE1–PE7): PE1, with a ‘head’ and flat ‘tail’; PE2, with the ‘head’ as in PE1 but the ‘tail’ with an additional frequency peak, sometimes exceeding the ‘head’; PE3, derivatives of PE1-chirps, produced in series such as pre-flight calls and extremely variable in frequency contour among individuals, but very specific and stereotyped within individuals (Fig. 2, PE3.1, PE3.2); PE4, with 2–4 extra frequency peaks after the ‘head’; PE5—like PE3 but with a pulsed ‘tail’; PE6, a chirp with a breaking voice, with two independent frequency components—the retained high juvenile frequency and the newly appearing low adult frequency, usually accompanying only the ‘tail’ part of the call; and PE7—adolescent adult-like calls, already lacking the high juvenile frequency component. For PE1-, PE3- and PE5-chirps, the Dur_{total} was 299 ± 59 ms, Dur_{beg-max} 85 ± 37 ms, Dur_{max-end} 214 ± 53 ms, ‘head’ duration 122 ± 43 ms, ‘tail’ duration 177 ± 57 ms, F_{beg} 2.54 ± 0.33 kHz, F_{end} 2.56 ± 0.26 kHz, F_{max} 3.67 ± 0.58 kHz, dF 1.21 ± 0.45 kHz (N=15 chicks of Ages 1–10; 5 males, 10 females, N=1945 calls, from 31 to 200 calls per chick).

Transitional chirp-to-trill calls

Transitional calls, consisting of both a chirp and a trill with at least two pulses, were given in various transitional contexts. We split these calls into two types: the PT1, transitional from PS-chirp to trill, and PT2, transitional from PE1-chirp to trill (Fig. 2 PT1, PT2, 3a, b).

2) Age-related shifts in call structures

Percentages of trills, PE- and PS-chirps and transitional calls at various Ages

To estimate the occurrence of trills, PE- and PS-chirps and transitional calls within and between Ages, we took a total of 23,309 calls, 133–200 calls per chick per Age, selecting them uniformly between the recording sessions (Table 1). Trills and transitional chirp-to-trill calls each comprised up to one third of all calls produced within the first four days of life (Age 1) and then declined steadily (see Fig. 4a). The percentage of PS-chirps was nearly constant at 20% throughout the first three months of life (Ages 1–7), but had nearly disappeared by the time of voice breaking (Ages 8–10), whereas the percentage of PE-chirps increased from the same 20% at Age 1 up to about 90% at Ages 9–10. Before voice breaking, beginning at Ages 8–10, only trills and PE-chirps remained in noticeable amounts and served as material for voice breaking and further transformation into the two definitive adult call types: pulsed, and non-pulsed. We studied the ontogenesis of these two “precursors” of the adult vocal repertoire in more detail.

Qualitative changes within the precursors (trills and PE-chirps) of two adult call types

To estimate qualitatively, the changes that trills undergo with age, we studied 1,214 trills (8–20 trills per chick per Age from four male and four female chicks; Table 1). During Ages 1 and 2, continuous T1- and T2-trills prevailed. During Age 3 these were displaced by broken-pulse T3-trills. During Ages 4–7 these were in turn replaced by W-shaped T4-trills, then by T5-trills, with some stroke-shaped pulses, then by perfectly stroked-pulsed T6-trills and finally during Age 9 by T7-trills containing both high juvenile, and low adult frequencies—characteristic of voice breaking (see Fig. 4b). Thus, for trills, the age trends lie in interspersing pulses with silent intervals alongside changes in the pulse shape, first to W-shaped and then to stroke-shaped, with finally the low adult frequency appearing alongside retained high juvenile frequency at the stage of voice breaking.

To estimate quantitatively, which changes the PE-chirps undergo with age, we analysed 1,127 calls, 11–20 PE-chirps per chick per Age from three male and four female chicks (Table 1). PE1 and PE2-chirps prevailed together up to Age 5, but during Ages 5–7, the PE1 percentage reached 93%, whereas PE2-chirps disappeared (Fig. 4c). During Age 4, PE3-chirps appeared in conjunction with preflight dis-

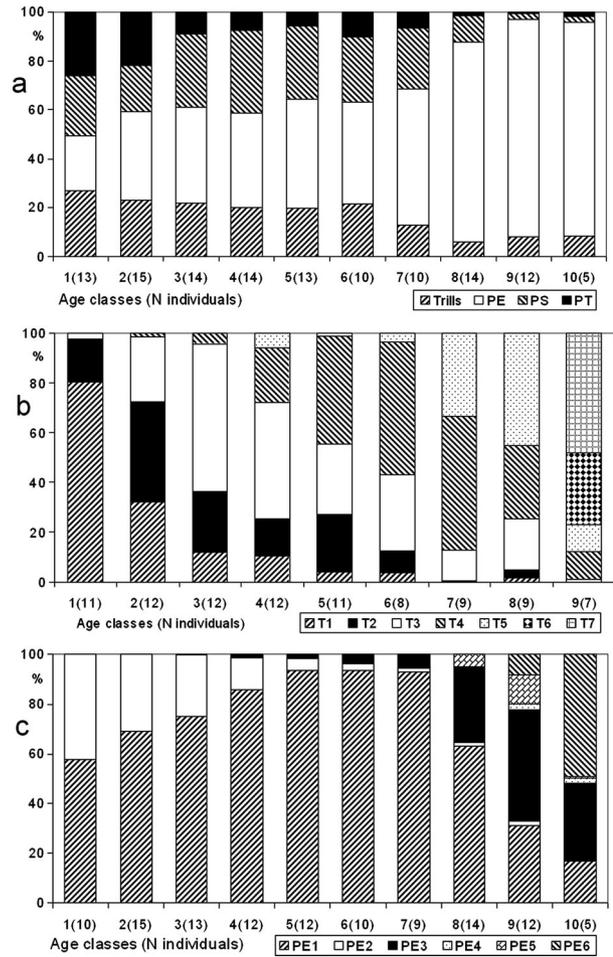


Fig 4. The occurrence of different call structures within and between age classes (“Ages”). Each bar represents one age class, and different shadings within each bar represent different call structures. The occurrence values are given in %. (a) The occurrence within and between age classes for trills (T), PE-chirps (PE), PS-chirps (PS) and transitional calls from chirp to trill (PT); (b) The occurrence within and between age classes for seven types of trills (T1–T7) and (c) The occurrence within and between age classes for six types of PE-chirps (PE1–PE6). For each age class, the samples of individuals, that provided calls for the analysis, are given in brackets.

plays, the percentage increasing to 50% by Age 9, and replacing PE1-chirps. Small percentages of PE4 chirps were found during Ages 9–10. PE5-chirps appeared during Age 8. PE6-type calls, characteristic of the voice breaking period, with both Juvenile (high) and adult (low) frequencies, appeared during Age 9, and reached about 50% during Age 10. Thus, for PE-chirps, the age trends are evidenced by the appearance of additional “waves” on the tail, sometimes exceeding the head, followed by the weakening and disappearance of the head, alongside the retention and

strengthening of the tail. As in the trills, during the period of voice breaking, chirps also have a low adult frequency component alongside the retained high juvenile frequency.

Thus, during voice breaking, adolescent calls show biphonation, according to Wilden et al.'s (1998) definition. The biphonic T7-trill (Fig. 2, 7) consists of two frequency components, one corresponding to the juvenile trill, ranging from 2.21 ± 0.39 to 3.94 ± 0.4 kHz (F_{\min} - F_{\max} for Age 9), and the other corresponding to the adult trill, below 1.5 kHz. The biphonic PE6-chirp (Fig. 2, 7) also consists of two independent fundamental frequencies. The frequency of the higher one ranges from 2.38 ± 0.27 to 4.4 ± 0.57 kHz (F_{\min} - F_{\max} for Age 9) and corresponds to the high juvenile frequency, whereas the frequency of the lower one ranges 0.6–1.3 kHz and corresponds to low adult call frequency. Thereafter, the retained juvenile frequency degrades, and the calls become monophonic, with only the low frequency present (PE7-chirps, T8-trills, Fig. 2).

3) Quantitative analysis of changes in the acoustic parameters of trills and PE-chirps, the precursors of adult call types

For the quantitative analysis, we used the same call samples as for the qualitative analysis of the trills and PE-chirps changing with age. For trills, F_{\max} values decreased steadily from Age 1 to Age 6 (Fig. 5a). From Age 7 onwards, the F_{\max} value increased progressively again and by Age 9 reached values similar to those at Age 1 (Age 1, $F_{\max} = 4.06 \pm 0.55$ kHz, $N = 155$; Age 9, $F_{\max} = 3.94 \pm 0.4$ kHz, $N = 105$; M-W test, $U = 6730.5$, $P < 0.05$). At the same time, the F_{\min} value was stable and never fell below 1.7 kHz up to Age 9, thereafter, however, average F_{\min} decreased to a minimum of 1.5 kHz (Fig. 5a). Up to and including Age 8, the F_{\min} value did not correlate significantly with age (Spearman rank correlations $R = -0.011$, $P = 0.71$, $df = 1109$), however, at Age 9 we observed a slight but significant decrease in the F_{\min} value (Age 8, $F_{\min} = 2.45 \pm 0.26$ kHz, $N = 124$; Age 9, $F_{\min} = 2.21 \pm 0.39$ kHz, $N = 105$; M-W test, $U = 3777$, $P < 0.001$). The decrease and subsequent increase in the F_{\max} value, alongside the relative constancy of the F_{\min} value, is similar to the F_{\max} age-related pattern of the dF trill values (not shown), with a lack of significant differences for dF values between Age 1 and Age 9 (Age 1, $dF = 1.76 \pm 0.43$ kHz, $N = 155$; Age 9, $dF = 1.72 \pm 0.45$ kHz, $N = 105$; M-W test, $U = 7552$, $P = 0.33$).

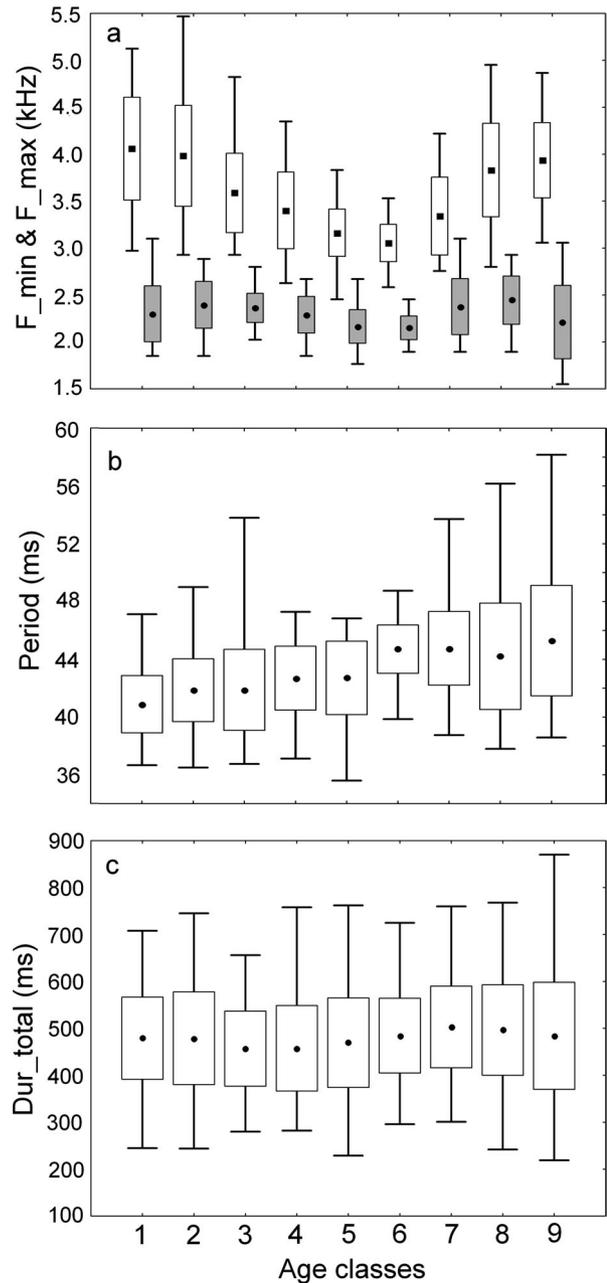


Fig. 5. Shifts in trill characteristics across Age classes 1–9, analyses for a pooled sample of calls taken from eight Red-crowned Crane chicks. (a) maximum (white boxes) and minimum (dark boxes) fundamental frequency; (b) Period; (c) total duration. The middle points show the averages, boxes—SD, whiskers—minimum and maximum values.

The temporal trill parameter showed a distinctive pattern of changes (Fig. 5b, c). Period increased steadily from 41 ± 2 ms at Age 1 to 45 ± 4 ms at Age 9 (Spearman rank correlations $R = 0.453$, $P < 0.001$, $df = 1212$). Trill duration showed a weak but signifi-

cant lengthening (Spearman rank correlations $R=0.072$, $P<0.05$, $df=1212$), however, the M-W test did not reveal any significant differences for Dur_{total} values between Age 1 and Age 9 (Age 1, $Dur_{total}=479\pm 87$ ms, $N=155$; Age 9, $Dur_{total}=484\pm 114$ ms, $N=105$, $U=8126.5$, $P=0.98$).

The pattern of frequency changes for PE-chirps was similar to that for trills (Fig. 6a). From Age 1 to Age 6, both F_{max} and dF values (not shown) decreased steadily. From Age 7, both the F_{max} and dF values increased, with a sudden increase during Ages 8–9. The M-W test revealed significant differences in F_{max} values between Ages 9 and 1 (Age 1, $F_{max}=3.81\pm 0.38$ kHz, $N=120$; Age 9, $F_{max}=4.4\pm 0.57$ kHz, $N=103$, $U=2500.5$, $P<0.001$). In contrast, the F_{min} values showed only a non-significant positive correlation with age (Spearman rank correlations $R=0.058$, $P=0.052$, $df=1127$), and no significant differences between Ages 1 and 9 (Age 1, $F_{min}=2.43\pm 0.2$ kHz, $N=120$; Age 9, $F_{min}=2.38\pm 0.27$ kHz, $N=103$; M-W test, $U=5728.5$, $P=0.347$). The F_{min} values of PE-chirps did not fall below 1.7 kHz (Ages 1–9), as was also the case for trills. The Dur_{total} values for PE-chirps showed a weak but significant increase with age (Spearman rank correlations $R=0.086$, $P<0.01$, $df=1125$, Fig. 6b), as was also the case for trills.

DISCUSSION

In our study of the Red-crowned Crane, we found that voice breaking results in the appearance of two adult call types, one derived from a chick trill, and the other from a chick chirp. These developmental traits occurred in both males and females.

For trills, age-related trends involved interspersing pulses with intervals of silence alongside which, pulse shapes changed from bell-shaped to stroke-shaped. This was followed by the appearance of the low adult frequency alongside the retained high juvenile frequency at the stage of voice breaking. The further disappearance of the juvenile trill component resulted in the development of the definitive adult call type: the “roll”.

For PE-chirps, age-related trends involved the weakening and disappearance of the “head” part of the frequency contour, along with the strengthening of the “tail” part and further appearance of the low adult frequency component while still retaining the high juvenile frequency during the stage of voice

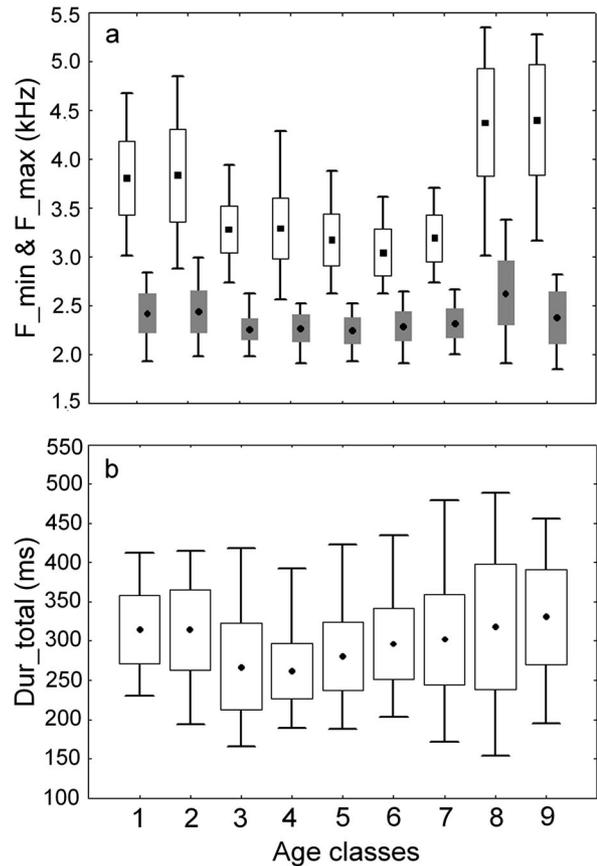


Fig. 6. Shifts in PE-chirp characteristics across Age classes 1–9, analyzed for a pooled sample of calls taken from seven Red-crowned Crane chicks. (a) maximum (white boxes) and minimum (dark boxes) fundamental frequency; (b) total duration. The middle points show the averages, boxes—SD, whiskers—minimum and maximum values.

breaking. Furthermore, the disappearance of the higher component resulted in formation of another definitive adult call type: the “yap”.

Trills, PE-chirps, transitional calls and one-humped PS-chirps, were all relatively abundant during the early age classes, but almost completely disappeared before voice breaking occurred, and none of them developed into an adult vocal type.

Our data indicate that the basic division into pulse and non-pulse structural patterns proposed by Niemeier (1979) for the Sandhill Crane, and for other crane species by other authors (Archibald 1976; Nesbitt & Bradley 1996; Budde 1999), may appear to be a “natural” classification for cranes. This is derived from the fact that each of the two distinctive structures, disposed on opposite ends of the gradual structural row of chicks calls (Fig. 3), arises into a distinctive adult call type after voice breaking (Fig. 2, T8

and PE7).

1) Stages of vocal ontogenesis of the Red-crowned Crane

There are four stages of vocal ontogenesis in the Red-crowned Crane, corresponding approximately to the four biologically relevant life stages of a growing chick (Fig. 7). During the first stage (Fig. 7a) corresponding to the beginning of Age 1 (hatching and 1–2 days spent close to the nest), we meet a few call types showing a row of gradual transitions from trill to chirp structure, with THE T1-trill call at the beginning of the row and PS2-chirp—at the end of the row. The PE1-chirp, which primarily functions as a food-begging call, is still lacking during Age 1, probably because the chicks still retain yolk sac reserves at this age, and are not yet hungry.

During the beginning of the second stage (Ages 2–7), the chicks become active, moving widely through their home range, and by the end of this stage the chicks become able to fly (Fig. 7b). During this

stage, the PE1-chirps appear and then prevail (Fig. 4a, c). Also, the structurally related PT2, PE2 and PS1 call types appear during this stage.

The third stage (Ages 8–9) corresponds to the phase of flight acquisition and, in wild cranes, to the subsequent migration to the wintering grounds (Fig. 7c). During this stage, young cranes acquire behavioural habits in relation to unfamiliar conspecifics in a flock, and for this purpose, the coordination of transitions, flights, foraging, resting and other activities is very important. Probably, in relation to this need, adolescent cranes develop new call types, such as preflight calls (PE3 with its structural variations PE3.1–PE3.2, PE5) and the disturbance-related call PE4 (Fig. 4c).

The fourth stage (Age 10, the beginning of voice breaking), corresponds to the break down of the parent-chick bond, which, in wild cranes, takes place during late winter on the wintering grounds and is accompanied by the appearance of both pulse and non-pulse biphonic calls with a second, low-frequency component, characteristic of the adult voice (Fig. 7d).

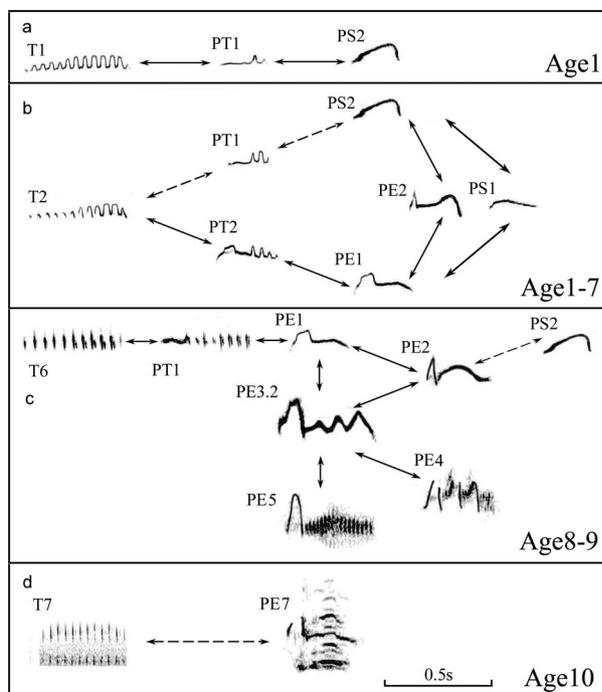


Fig. 7. Four stages of vocal ontogenesis of the Red-crowned Crane: (a) from hatching to 1–2 days; (b) from commencing active movement in the home range to acquiring flight capability; (c) completion of flight ability acquisition and migration to the wintering grounds; (d) the break down of the parent-chick bond, the beginning of voice breaking. The arrows show structural transitions between call types. All spectrograms were created with the same time and frequency scales.

2) Age shifts in call parameters and a proposed function for the retention of the high juvenile call frequency

Our data for the Red-crowned Crane agree with evidence in the literature for other crane species, that the juvenile call frequency is retained as the chicks grow, and that the low-frequency, adult component arises suddenly during the phase of voice breaking (Niemeier 1979; Gebauer & Kaiser 1998). Both the trill and PE-chirp fundamental frequencies remained above 1.5 kHz up to voice breaking (Fig. 5a, 6a). The body weight of chicks increased about 50-fold from 0.15 kg (N=56) on hatching to 7.32 kg (N=52) at 110 days old (Age 8) (Postelnykh & Kashentseva 2005), and by 110 days tracheal elongation has already finished. We measured the trachea of one four-month old female Red-crowned Crane, which died in an accident, and found it to be 84 cm, or nearly twice the length of the bird's neck. Similar trends in body growth, and corresponding growth of the syrinx and trachea were also reported for the Sandhill Crane by Niemeier (1979). However, the substantial changes in body size and vocal apparatus did not correlate with the start of voice breaking, which occurs much later both in Sandhill and in Red-crowned cranes. This discrepancy may be explained partly by the rather stable thickness of some parts of the syringeal membranes, regardless of age, reported in particular for the Sand-

hill Crane (Niemeier 1979). Mammalian bioacoustic studies have shown that the fundamental frequency of a call depends not only on thickness, but more importantly on the length of the vibrating portion of the vocal folds (Titze 1994). Thus, other conditions being equal, larger or longer vibrating structures should produce lower fundamental frequencies (Fitch & Hauser 2002). As both the syrinx and the vibrating structure grow with age in the Sandhill Crane, it seems reasonable to expect corresponding enlargement with age also in the Red-crowned Crane. Since both of these crane species retain juvenile call frequencies until voice breaking at 9–10 months of age (Niemeier 1979, present data), we propose that crane chicks use some kind of tuning of the syringeal membranes to maintain the call frequency within a restricted frequency range. Although the mechanisms for such tuning are still unclear, we propose that crane chicks may actively manipulate elements of their vocal apparatus, adjusting the fundamental frequency of their calls by varying the length of the vibrating portion of the syringeal membranes, the degree of their stretching, or perhaps subsyringeal pressure. Such manipulation would allow chicks to override any direct relationship between syrinx size and call frequency, however, physiological research is necessary to test this hypothesis. Among humans, the comparable ability of varying the vowel frequency during singing, for example, with transition to falsetto, has been reported (Fitch & Hauser 1995).

The results of this study provide useful material for the discussion of the probable evolutionary pressures involved in retaining high juvenile frequencies for a prolonged period. Our unpublished data on the start, end, and duration of voice breaking among our captive cranes lead us to suggest that the break down of the parent-chick bond may be the key factor, triggering voice breaking. The dates of voice breaking varied greatly among individual chicks in our study. In one of six chicks examined here, voice breaking started at five months of age, in four others it occurred at seven months, and in the sixth it occurred at 10 months. By 9–10 months of age five of the chicks developed definitive adult calls, while the sixth chick took 10.5 months.

It appears, that the earlier dates of voice breaking in our study in comparison with those reported by other authors (9–11 months of age, Archibald 1976; Niemeier 1979; Gebauer & Kaiser 1998) were related to the earlier timing of parent-chick separation in captivity. The chick with the earliest beginning of

voice breaking, at five months old, was separated from its parents at 3.5 months; conversely, the chick with latest start of voice breaking, was separated from its parents at 10 months of age, and subsequently developed adult calls within 2–3 weeks. We hypothesize, therefore, that voice breaking is directly related to the breakdown of the parent-chick bond and to the independence of the adolescents. From a functional perspective, the retained high frequency calls may represent an infantile characteristic, essential to evoking parental care for the growing chick (Morton 1977; Owings & Morton 1998). Wild Red-crowned Cranes continue to take care of their chicks during the autumn migration and on the wintering grounds, only beginning to drive them away shortly before the new breeding season commences (Archibald 1976; Kamata 1994). During migration and winter, adolescent cranes live with their parents in flocks numbering up to several hundred individuals (Seong-Hwan & Won 1994; Swengel 1996), sometimes of several species, thus the high-frequency infantile calls may also act as a mechanism to reduce intra- and even inter-specific aggression from other adult cranes.

Additional data are necessary to confirm whether the timing of the breakdown of the parent-chick bond indeed affects the timing of voice breaking, or whether the start of this stage is individual-dependent.

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