

Voice breaking in adolescent red-crowned cranes (*Grus japonensis*)

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Summary

Voice breaking is a process associated with puberty of human males that also occurs in adolescence in some birds. This study reports the jump-like vocal changes occurring during voice breaking in adolescent red-crowned cranes (*Grus japonensis*). We investigated acoustic parameters of chirp and trill calls during vocal ontogenesis from hatching to the age of 1.5 years in 17 male and 31 female captive red-crowned cranes and compared them with definitive calls of 5 male and 8 female conspecific adults. During voice breaking, trills and chirps of both sexes contained two non-overlapping independent fundamental frequencies: the upper one, representing the retained juvenile frequency, and the lower one, the newly attained adult frequency. Before voice breaking, the calls contained only the upper frequency, whereas after it only the lower one. Voice breaking occurred between the age of 7 and 11.5 months. We test whether sex, dates of birth and body mass gain are associated with voice breaking and speculate whether voice breaking triggers the disruption of the parent–chick bond or *vice versa*, or both events are driven by a third, yet unidentified trigger.

Keywords: vocal development, nonlinear phenomena, acoustic communication, maturation, call ontogenesis.

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Introduction

In avian research focused on vocal development from hatching to maturation, the primary distinction should be drawn between birds, experiencing and not experiencing vocal learning. For instance, passerines (Kroodsma & Baylis, 1982; Marler & Peters, 1982; Catchpole & Slater, 2008), parrots (Britten-Powell et al., 1997; Bond & Diamond, 2005) and hummingbirds (Jarvis et al., 2000; Jarvis, 2004) acquire adult vocal patterns when they listen to vocalizations of other, usually conspecific adults. On the other hand, many bird taxa do not experience vocal learning. However, the self-extracting programs of vocal development are by no means identical across these birds. In particular, acoustic characteristics, mainly the fundamental frequency, can either change gradually with age, as in geese (Würdinger, 1970; ten Thoren & Bergmann, 1986, 1987) and doves (Ballintijn & ten Cate, 1997), or drop abruptly during a short period of time, as in cranes (Niemeier, 1979; Gebauer & Kaiser, 1998), American coots *Fulica americana* (Cosens, 1981) and green woodhoopoes *Phoeniculus purpureus* (Radford, 2004). This jump-like fall in the fundamental frequency has been referred to as ‘voice breaking’, for its similarity to voice changes occurring in male humans at puberty (Niemeier, 1979; Abs, 1980; Gebauer & Kaiser, 1998; Radford, 2004). Similarly to humans (e.g., Fitch & Giedd, 1999; Lee et al., 1999), associations of voice breaking with sex, body size and maturation have been shown for two bird species (Cosens, 1981; Radford, 2004).

The first mention about crane’s voice breaking goes back to the thirteenth century, when German Emperor Friedrich II noted in his book on the falconry “*De arte venandi cum avibus*” (1248) the strange voice changes occurring in adolescent cranes. Much later, Heinroth (1927) described the voices of 8-month-old cranes during voice breaking as sounding alternately as squeaks or as drumbeats. More recent studies in a few crane species (Archibald, 1976; Niemeier, 1979; Nesbitt & Bradley, 1996; Gebauer & Kaiser, 1998) report different terms of its onset, completion and duration. Also, they report that long before voice breaking, at the age of 3–4 months, fundamental frequencies of crane vocalizations are still kept above 2–4 kHz, whereas at the age of 1 year they already do not exceed 1–1.2 kHz (sandhill crane, *Grus canadensis*: Niemeier, 1979; Nesbitt & Bradley, 1996; Eurasian crane, *Grus grus*: Gebauer & Kaiser, 1998; grey crowned crane, *Balearica regulorum*: Budde, 1999a,b, 2001); Siberian crane, *Grus leucogeranus*: Kasirova et al.,

2005; Bragina & Beme, 2007; red-crowned crane: Klenova et al., 2007, 2008, 2009). Summarizing these findings, voice breaking occurs between the ages of 3–4 months and 1 year, but the voice changes occurring during this age have not yet been studied in details in any crane species.

Among cranes, the early vocal development has been studied most thoroughly in the red-crowned crane. The vocal repertoire of red-crowned crane chicks contains chirps and trills, and the vocal ontogenesis for these vocalizations is similar in both sexes, with the same call types occurring in males and females and with very weak intersexual differences in call characteristics (Klenova et al., 2007, 2008, 2009).

The red-crowned crane is one of the rarest crane species, the population in nature estimated at ca. 2100 birds (Archibald, 2003). Both parents raise one or two chicks, leaving the nest soon after hatching (Masatomi, 1981; Vinitser, 1981). The parent–chick social bond is maintained up to 8–10.5 months, and breaks as late as in the wintering grounds, before the next breeding season (Kamata, 1994; Archibald & Lewis, 1996).

The purposes of this study were (1) to describe in further detail the qualitative and quantitative changes occurring with chirps and trills during voice breaking in the red-crowned crane (2) to compare calls during voice breaking with earlier chick calls and with definitive adult calls and (3) to test whether sex, dates of birth and body mass gain are associated with voice breaking.

Materials and methods

Study birds, dates and sites

The red-crowned crane calls were recorded in 2003–2008 from 61 individuals: 48 chicks (17 male, 31 female) of various age, from 4 days to 1.5 years old, and from 13 adults (5 male, 8 female) over 6 years of age. The chicks' hatching dates ranged from 12 May to 22 July. Fourteen of the chicks were raised by their own or conspecific adoptive parents and the 31 chicks were human-raised in Oka Crane Breeding Centre of Oka Biosphere State Nature Reserve (Ryazan region, Russia). The remaining 3 chicks were parent-raised in Moscow Zoo (Moscow, Russia). Nine of the 13 adults were kept at Oka Crane Breeding Centre, 2 adults were kept at Rare Bird Reintroduction Station of Khingansky State Nature Reserve (Amur region, Russia); the remaining 2 adults were kept at St. Petersburg and Novosibirsk Zoos (Russia). Six

of the 13 adults were wild-captured at various ages; the remaining 7 birds were raised in captivity.

Cranes were housed in approx. 100-m² enclosures covered with grass, trees and bushes. Chicks were kept with their parents or in groups of 2–8 conspecific chicks; adults were kept in male–female pairs or in families with 1–2 of their own or adoptive chicks. The study birds were sexed either by their behaviour or with DNA PCR-amplification (Griffiths et al., 1998) and individually marked with leg rings.

Call recordings

We recorded calls in the morning or in the evening, at time of the highest activity of cranes. Each recording of a particular crane lasted 45–60 min and was separated from another recording of the same bird by ≥ 24 h. During a recording session, lasting for 3–7 days, we made 1–4 recordings per bird. During the study, some birds were recorded only once, while others several times (up to 12 recording sessions per bird). Successive recording sessions of individual birds were separated by 1–3 months.

We used a Marantz PMD-222 cassette recorder (D&M Professional, Kanagawa, Japan) with a Sennheiser K6-ME67 shotgun condenser microphone (Sennheiser Electronic, Wedemark, Germany), and Emtec-CS II Type II chrome audiocassettes (Emtec Consumer Media, Ludwigshafen, Germany). The system had a frequency response of 0.04–14 kHz at a tape speed of 4.75 mm/s. Distance from a bird to the microphone was 1.5–15 m.

Successive record digitizing at 22.05 kHz and 16 bit precision, low-pass filtration at 6.0 kHz, downsampling to 11.025 kHz, creation of spectrograms (512-point Hamming window, frame 50%, overlap 96.87%, providing time resolution 1.5 ms and frequency resolution 21 Hz) and measurements were made with Avisoft-SASLab Pro v. 4.3 (Avisoft Bioacoustics, Berlin, Germany). We classified calls according to presence or absence of pulsation into trills or chirps and selected for further analysis chirps with bi-part ('head' and 'tail') contour of frequency modulation (PE-chirps according to Klenova et al., 2007, hereafter 'chirps') and all trills (Figure 1). Only PE-chirps and trills occurred all over the vocal ontogenesis (Klenova et al., 2007, 2009).

Call analysis

We used two independent call samples for two different analyses. With the first sample, we estimated changes in acoustic characteristics of calls along

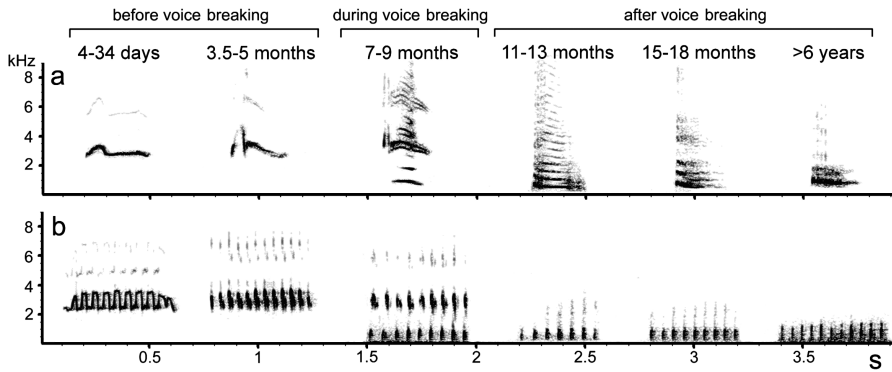


Figure 1. Spectrogram of chirps (a) and trills (b) illustrating call patterns occurring before, during and after voice breaking in red-crowned cranes. (a) First 5 chirps were recorded from the female No. 50 during her ontogenesis; the 6th chirp was recorded from the adult female No. 101. (b) First 5 trills were recorded from the male No. 48 during his ontogenesis; the 6th trill was recorded from the adult male No. 100.

the ontogenesis. This sample included chirps of 57 cranes and trills of 48 cranes (in total, calls of 61 cranes were available for this analysis) in 6 age classes: 4–34 days, 3.5–5 months, 7–9 months, 11–13 months, 15–18 months and >6 years. Each age class contained different cranes, 7–10 individuals (3–5 males and 4–7 females) per age class for chirps and 6–10 individuals (3–5 males and 3–7 females) per age class for trills. We selected for analysis 1–2 recording sessions per bird. To avoid pseudoreplication, we included calls from different recordings within a recording session or from different parts within recording where only one recording per bird was available. We measured acoustic parameters of 12–20 chirps and 4–20 trills per bird, 1132 chirps and 811 trills in total.

For each call, we measured the duration and the frequency of maximum intensity. For each trill, we calculated additionally the mean pulse period (Period) as the total duration of 5–12 successive pulses (measured as the duration from the beginning of a preceding pulse to the beginning of the following pulse) divided by the number of pulses. For each chirp, we measured additionally the minimum fundamental frequency and the maximum fundamental frequency from the screen with the reticule cursor at the spectrogram window of Avisoft. For each bird we calculated mean values for each acoustic parameter.

With the second sample, we estimated the approximate onset, completion and duration of voice breaking. This sample included calls of 24 chicks

(9 male and 15 female, 7 parent-raised and 17 human-raised), which provided call recordings from hatching up to 1.5 years. We selected for analysis 6–12 recording sessions per chick, separated by 1–3 months, containing at least 100 calls, either trills or chirps, noise-free. For each chick, we checked visually by spectrograms, waveforms and mean power spectra for the appearance and disappearance of specific patterns of trills and chirps labeling the dates of onset and completion of voice breaking. In total, we checked over 24 000 calls from the 24 individuals, 600–1200 calls per crane.

Body mass measurement

Body mass measurements were made in 2002–2008 at Oka Crane Breeding Centre for the same sample of 10 adults (5 males, 5 females) which provided call recordings and for independent (except one individual) samples of 11 chicks (5 male, 6 female) from hatching to 7 months, and of 9 (4 male, 5 female) 16 month old cranes. Chicks were weighted on the day of hatching and than at the age of 30, 60, 90, 120, 150, 180, and 210 days. Body mass measurements (to the nearest 10 g) were made by Kern De 15K5 balance (Kern & Sohn, Balingen-Frommern, Germany).

Statistical analyses

All the analyses were carried out with the statistical package STATISTICA 6.0 (StatSoft, Tulsa, OK, USA). All tests were two tailed; all means are given as mean $\pm$ SD and differences are considered significant where $p < 0.05$. We used a one-way ANOVA with Tukey HSD post-hoc tests to compare the acoustic parameter values across age classes, as the distribution did not violate the normality assumption at any age (Kolmogorov–Smirnov test, $p > 0.05$). Also, we used one-way ANOVA with Tukey HSD post-hoc tests to compare the body mass values across cranes of different ages, as the distribution did not differ from normal at any age (Kolmogorov–Smirnov test, $p > 0.05$). We used a GLM ANOVA to estimate the effects of sex and hatching date on the onset and completion of voice breaking, with sex introduced as a categorical variable, and hatching date as a continuous variable.

Results

Chirp and trill patterns labeling voice breaking

Chirps

The stage of high-frequency chirps (before voice breaking). At this stage, spanned from hatching up to voice breaking, we observed a single chirp pattern. It contained only the upper fundamental frequency f_0 , with well-expressed 'head' and 'tail' parts in its bi-partial contour of frequency modulation (Figure 1a, first two calls).

The stage of two-frequency chirps (during voice breaking). Within this stage, we observed three distinctive chirp patterns, replacing one another sequentially. The early pattern contained a well-expressed f_0 . The newly appeared lower fundamental frequency g_0 was very short in duration (Figure 2a). Within a call, the f_0 and g_0 either followed one another or occurred simultaneously.

The medium pattern contained the retained juvenile f_0 band, but the g_0 was already nearly as long as the 'tail' part of a call contour. The f_0 and g_0 occurred only simultaneously, often resulting in the appearance of linear combinatory frequency bands (Figure 1a, third call; Figure 2b). The maximum intensity band was either the f_0 or g_0 .

The late pattern contained the g_0 band longer in duration than those of the f_0 . The f_0 band became poorly visible and lost the 'tail' part of its contour (Figure 2c). The f_0 usually preceded the g_0 (Figure 2c). The band of maximum intensity was always the g_0 band. We did not find any two-frequency chirp, where the f_0 and g_0 values overlapped in frequency.

The stage of low-frequency chirps (after voice breaking). Within this stage, we observed only chirps, containing nothing but the g_0 band (Figure 1a, last three calls).

Trills

The stage of high-frequency trills (before voice breaking). At this stage, spanned from hatching up to voice breaking, we observed only trills containing the upper fundamental frequency band f_0 singly; however, its contour underwent shifts within this stage (Figure 1b, first two calls).

The stage of two-frequency trills (during voice breaking). Within this stage, we observed the newly appeared lower fundamental frequency g_0

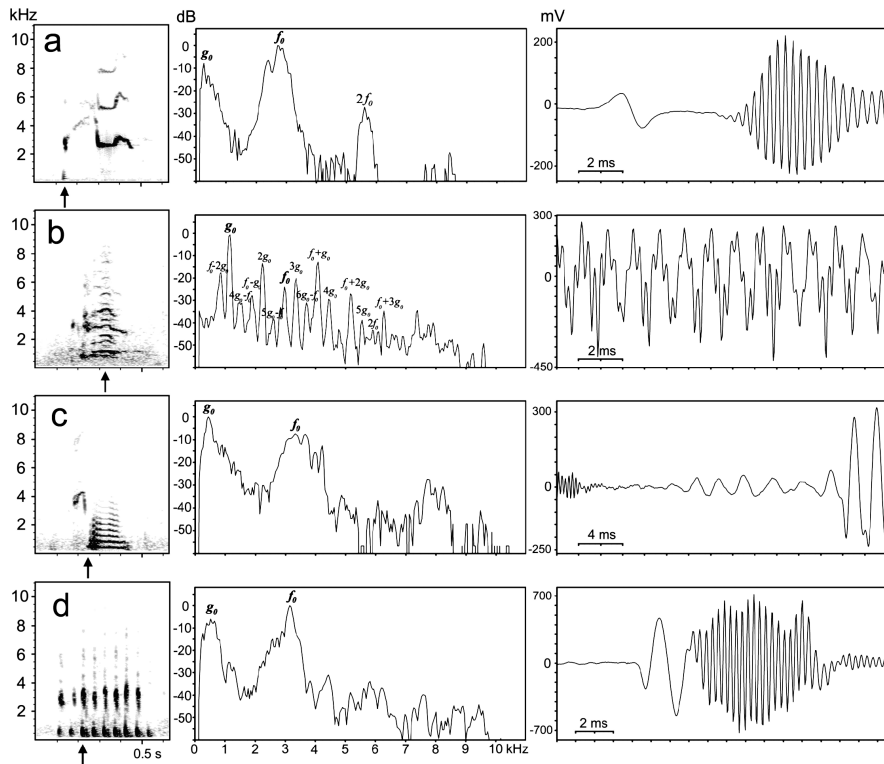


Figure 2. Spectrograms, power spectra and waveforms illustrating patterns of chirps and trills labeling voice breaking. (a) two-frequency chirp with a newly appeared short fundamental frequency g_0 and a well-expressed fundamental frequency f_0 , one after another; (b) two-frequency chirp with two fundamental frequencies f_0 and g_0 occurring simultaneously that resulted in their interaction with appearance of linear combinatory frequency bands; (c) two-frequency chirp with a short fundamental frequency f_0 and already well-expressed fundamental frequency g_0 , one after another; (d) two-frequency trill with the fundamental frequency g_0 and the fundamental frequency f_0 , one after another. Arrows indicate call parts of 15 ms (a, b, d) or 30 ms (c) from which the frequency spectra and waveforms were created. Spectrograms were created at sampling rate of 22.05 kHz, 512-point Hamming window, frame 50%, and overlap 96.87%. These settings provided time resolution of 0.75 ms and frequency resolution of 43 Hz.

alongside with already present upper fundamental frequency f_0 (Figure 1b, third call; Figure 2d). Within a call, the f_0 and g_0 either followed one another (Figure 2d) or occurred simultaneously and interacted within each trill pulse. We did not find any two-frequency trill, where the f_0 and g_0 overlapped in frequency.

The stage of low-frequency trills (after voice breaking). At this stage, we only observed trills consisting of nothing but the g_0 band (Figure 1b, last three calls). We can conclude that, during voice breaking, both juvenile chirps and juvenile trills transformed into the adult calls and they did so via the stage of two-frequency calls.

Acoustic characteristics of chirps and trills during the early vocal ontogenesis

Chirps

Analysis of acoustic parameters confirmed the results of visual inspection of call spectrograms: both the f_0 values (range 2.2–5.1 kHz) and the g_0 values (range 0.3–1.0 kHz) of chirps were nearly age-independent (Table 1). We did not find any single chirp with the f_0 and the g_0 frequencies overlapping. ANOVA revealed a significant age effect on the duration of chirps (Table 1). The duration decreased significantly with transition from high-frequency chirps (age classes 4–34 days, 3.5–5 months) to two-frequency chirps (7–9 months) and with transition from two-frequency chirps to low-frequency chirps (11–13 months and older). At the same time, the f_0 values of high-frequency chirps and of two-frequency chirps were very close to each other (Table 1). Post-hoc Tukey HSD test did not reveal significant differences either in the $f_{0,\max}$ of high-frequency chirps at 3.5–5 months and those of two-frequency chirps at 7–9 months ($p = 0.98$), or in the $f_{0,\min}$ of high-frequency chirps at 4–34 days and those of two-frequency chirps at 7–9 months ($p = 0.87$). Similarly, the $f_{0,\text{peak}}$ values did not differ significantly between high-frequency and two-frequency chirps (Table 1).

The g_0 values of two-frequency chirps (7–9 months) and of low-frequency chirps (11–13 months and older) were also very close to each other (Table 1). However, distinctive to the f_0 , the g_0 decreased slightly but significantly with transition from two-frequency chirps to low-frequency chirps at 15–18 months (post-hoc Tukey HSD test, $p = 0.002$, $p < 0.001$ and $p = 0.016$ for the $g_{0,\max}$, $g_{0,\min}$ and $g_{0,\text{peak}}$, respectively). At the same time, the $g_{0,\max}$ and the $g_{0,\text{peak}}$ of two-frequency chirps at 7–9 months did not differ significantly from low-frequency chirps at 11–13 months (post-hoc Tukey HSD test, $p > 0.05$ in both cases); and the $g_{0,\text{peak}}$ of two-frequency chirps at 7–9 months did not differ from those of low-frequency chirps at the age of >6 years (post-hoc Tukey HSD test, $p = 0.75$). We can conclude that the

Table 1. Mean $\pm$ SD values for temporal and frequency parameters of chirps of 57 red-crowned cranes of six age classes, and one-way ANOVA results of comparison between age classes.

Chirp parameter	Age class (<i>N</i> birds)					ANOVA results	
	High-frequency chirp		Two-frequency chirp				
	Low-frequency chirp						
	4–34 days (10)	3.5–5 months (10)	7–9 months (10)	11–13 months (7)	15–18 months (10)		>6 years (10)
Duration (ms)	334 ± 43 ^a	341 ± 51 ^a	245 ± 58 ^b	161 ± 35 ^c	144 ± 25 ^c	125 ± 23 ^c	$F_{5,51} = 52.7$ $p < 0.001$
$f_{0,\text{max}}$ (kHz)	3.75 ± 0.44 ^a	4.39 ± 0.34 ^b	4.35 ± 0.60 ^b				$F_{2,27} = 5.9$ $p = 0.008$
$f_{0,\text{min}}$ (kHz)	2.49 ± 0.22 ^a	2.87 ± 0.25 ^b	2.54 ± 0.28 ^a				$F_{2,27} = 6.8$ $p = 0.004$
$f_{0,\text{peak}}$ (kHz)	2.98 ± 0.34 ^a	3.16 ± 0.27 ^a	2.99 ± 0.37 ^a				$F_{2,27} = 0.9$ $p = 0.42$
$g_{0,\text{max}}$ (kHz)			0.89 ± 0.08 ^a	0.77 ± 0.12 ^{a,b}	0.71 ± 0.11 ^b	0.73 ± 0.09 ^b	$F_{3,33} = 6.3$ $p = 0.002$
$g_{0,\text{min}}$ (kHz)			0.65 ± 0.12 ^a	0.45 ± 0.09 ^b	0.41 ± 0.08 ^b	0.45 ± 0.06 ^b	$F_{3,33} = 13.6$ $p < 0.001$
$g_{0,\text{peak}}$ (kHz)			0.76 ± 0.10 ^a	0.64 ± 0.12 ^{a,b}	0.60 ± 0.12 ^b	0.71 ± 0.11 ^{a,b}	$F_{3,33} = 3.9$ $p = 0.018$

The same superscripts indicate which age classes did not differ significantly ($p > 0.05$, Tukey HSD post-hoc test).

f_0 of high-frequency chirps and the f_0 of two-frequency chirps were found lying within the same range of values in chicks and adolescents (up to 7–9 months), while the g_0 of two-frequency chirps and the g_0 of low-frequency chirps were within the same range of values in adolescents and adults (7–9 months and older).

Trills

Analysis of acoustic parameters confirmed the results of visual inspection of call spectrograms: both the f_0 values (range 2.4–3.7 kHz) and the g_0 values (range 0.4–0.8 kHz) of trills were nearly age-independent (Table 2). We did not find any single trill with the f_0 and the g_0 frequencies overlapping. One-way ANOVA did not reveal a significant age effect on trill duration (Table 2). The Period increased significantly with transition from high-frequency trills at 4–34 days and 3.5–5 months, to two-frequency trills at 7–9 months (post-hoc Tukey HSD test, $p < 0.001$ and $p = 0.034$ respectively), but remained stable at transition to low-frequency trills at older age (post-hoc Tukey HSD test, $p > 0.13$ for all the three comparisons). The $f_{0,\text{peak}}$ of two-frequency trills at 7–9 months differed significantly from those of high-frequency trills at 3.5–5 months (post-hoc Tukey test, $p = 0.011$), but did not differ from the $f_{0,\text{peak}}$ at 4–34 days (post-hoc Tukey HSD test, $p = 0.44$). No significant difference was found in the $g_{0,\text{peak}}$ between two-frequency trills and low-frequency trills in any comparison (Table 2). We can conclude that, similarly to chirps, f_0 of high-frequency trills and two-frequency trills were within the same range in chicks and adolescents (up to 7–9 months), while g_0 of two-frequency trills and low-frequency trills were within the same range in adolescents and adults (7–9 months and older).

Onset, completion and duration of voice breaking

We assumed that voice breaking is the period when two-frequency chirps and/or two-frequency trills occurred together with other vocalizations. The onset of voice breaking was assumed to be the date of the first recording which contained at least one two-frequency chirp or two-frequency trill, while the completion was assumed to be the date of the first recording lacking two-frequency chirps and two-frequency trills and containing only low-frequency chirps and low-frequency trills. Between individuals, the age of onset ranged from 3.5 to 11 months, and the age of completion ranged from

Table 2. Mean $\pm$ SD values for temporal and frequency parameters of trills of 48 red-crowned cranes of six age classes, and one-way ANOVA results of comparison between age classes.

Trill parameter	Age class (<i>N</i> birds)						ANOVA results
	High-frequency trill		Two-frequency trill		Low-frequency trill		
	4–34 days (10)	3.5–5 months (10)	7–9 months (7)	11–13 months (7)	15–18 months (6)	>6 years (8)	
Duration (ms)	420 ± 90 ^a	493 ± 105 ^a	401 ± 32 ^a	486 ± 97 ^a	425 ± 31 ^a	466 ± 12 ^a	$F_{5,42} = 1.5$ $p = 0.222$
Period (ms)	43 ± 4 ^a	47 ± 4 ^{a,c}	54 ± 5 ^b	51 ± 6 ^{b,c}	49 ± 2 ^{a,b}	48 ± 3 ^{a,b}	$F_{5,42} = 5.8$ $p < 0.001$
$f_{0, \text{peak}}$ (kHz)	2.78 ± 0.19 ^a	3.21 ± 0.35 ^b	2.96 ± 0.37 ^a				$F_{2,24} = 5.1$ $p = 0.015$
$g_{0, \text{peak}}$ (kHz)			0.55 ± 0.08 ^a	0.54 ± 0.12 ^a	0.67 ± 0.03 ^a	0.60 ± 0.15 ^a	$F_{3,24} = 2.1$ $p = 0.127$

The same superscripts indicate which age classes did not differ significantly ($p > 0.05$, Tukey HSD post-hoc test).

Table 3. Mean $\pm$ SD values and GLM results for age of onset and completion and the duration of voice breaking in 24 red-crowned cranes.

Voice breaking	♂♂ (<i>N</i> = 9)	♀♀ (<i>N</i> = 15)	All cranes (<i>N</i> = 24)	Sex effect	Hatching date effect
Onset (days)	184 $\pm$ 53	229 $\pm$ 58	212 $\pm$ 60	$F_{1,21} = 0.34$ $p = 0.57$	$F_{1,21} = 3.39$ $p = 0.08$
Completion (days)	361 $\pm$ 31	340 $\pm$ 36	347 $\pm$ 35	$F_{1,19} = 0.91$ $p = 0.35$	$F_{1,19} = 2.19$ $p = 0.16$
Duration (days)	169 $\pm$ 47	119 $\pm$ 65	137 $\pm$ 63	$F_{1,19} = 0.03$ $p = 0.86$	$F_{1,19} = 3.61$ $p = 0.07$

8.7 to 13.5 months. The duration of voice breaking was, thus, 1–8.5 months. The average duration of voice breaking was 4.6 months, the average age of onset 7.1 months and the average age of completion 11.6 months (Table 3). No significant sex effect was found for the onset, completion or duration of voice breaking, even though males started it on average earlier, completed later and lasted it longer than females. Similarly, no significant effects of date of hatching were found on the onset, completion or duration of voice breaking (Table 3).

Voice breaking and body mass gain

At hatching, body mass was 0.15 ± 0.02 kg, increased rapidly to the age of 5 months and then continued increasing at a very slow rate (Figure 3). Although the chicks' body mass increased significantly with age (one-way ANOVA, $F_{9,106} = 171.8$, $p < 0.001$), we did not find significant differences in body mass in all comparisons between ages older than 5 months (Figure 3). For example, body mass of 5-month-old cranes (8.50 ± 1.07 kg) did not differ significantly from the mass of 7 month-old ones (9.38 ± 1.23 kg, post-hoc Tukey HSD test, $p = 0.30$) and from the mass of adults (9.09 ± 0.80 kg, post-hoc Tukey HSD test, $p = 0.83$). Thus, the age of onset of voice breaking coincides approximately with the age of termination of body mass gain (Figure 3). The age of onset of voice breaking varied stronger compared to completion, probably due to individual variation in body mass gain rate.

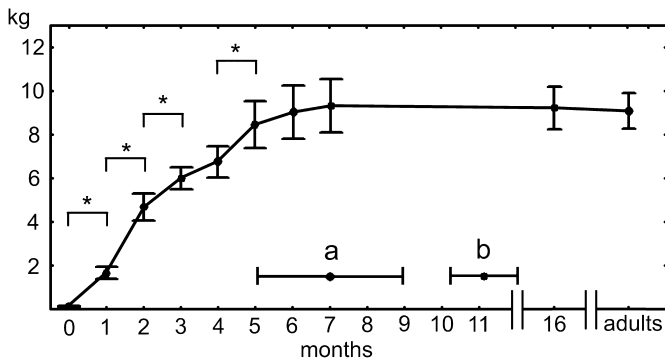


Figure 3. Body mass gain with age and approximate age of onset and completion of voice breaking in red-crowned cranes. Points show Means, whiskers show SE, Asterisk shows significant difference (post-hoc Tukey HSD test, $p < 0.05$) in body mass between ages. (a) Mean $\pm$ SE age of onset of voice breaking; (b) mean $\pm$ SE age of completion of voice breaking in red-crowned cranes.

Discussion

Jump-like vocal development

In the red-crowned crane we observed the jump-like transition from high-frequency juvenile calls to low-frequency adult-like calls through the stage of two-frequency calls. The upper and the lower frequencies were kept each within a limited range of values. Voice breaking represented a phase of vocal ontogenesis when both the upper and lower fundamental frequencies could occur within a call and was similar between sexes.

A similar jump-like, but sex-specific vocal development has been reported for American coots (Cosens, 1981) and green woodhoopoes (Radford, 2004). At the age of 1.5 months, female but not male American coots (females are larger in this species) change fundamental frequencies of their calls from 1.6 kHz to 0.7 kHz. Similarly, when 3–5 months old, male, but not female, green woodhoopoes (males are larger) change fundamental frequencies of their calls from 0.8 kHz to 0.5 kHz. Similarly to red-crowned cranes, no intermediate fundamental frequencies between the upper and lower ones were found in either species. However unlike in the red-crowned cranes, no two-frequency calls were reported for these species, and voice breaking occurred only in the larger sex (Cosens, 1981; Radford, 2004).

Voice breaking via a transitional phase of two-frequency calls can be expected to occur also in other crane species. For instance, in the sandhill,

Eurasian, grey crowned and Siberian cranes the upper fundamental frequencies range from 2 to 4 kHz during the first 3–4 months of life, whereas at 1 year and older the fundamental frequency lies below 1–1.2 kHz (Niemeier, 1979; Nesbitt & Bradley, 1996; Gebauer & Kaiser, 1998; Budde, 1999a,b, 2001; Kasirova et al., 2005; Bragina & Beme, 2007). Potentially, voice breaking can also occur in Procellariiformes and Charadriiformes. For instance, high juvenile fundamental frequency of 4 kHz retaining until fledgling was reported for the Leach's storm-petrel *Oceanodroma leucorhoa* (Naugler & Smith, 1992) and those of 2 kHz for the brown noddly *Anous stolidus* (Riska, 1986a), whereas the adult fundamental frequencies are 1–1.2 kHz in both species (Riska, 1986b; Taoka et al., 1989).

It remains unclear how the full-grown adolescent red-crowned cranes are able to keep their high fundamental frequency within the same range of values as newly-hatched chicks. The detailed anatomical investigation of vocal-producing structures undertaken by Niemeier (1979) based on several syrinx specimens taken from sandhill cranes of different ages failed to find any age-dependent relations in size, area or thickness of tympaniform membranes. Internal and external tympaniform membranes within the syrinx had a stable thickness up to 2 years of age, with high individual variation (Niemeier, 1979). Also, the tracheal elongation of cranes does not influence the fundamental frequency of their calls (Niemeier, 1979; Fitch, 1999). The trachea length from syrinx to the angle of the beak of two red-crowned crane females that died accidentally at the age of 4 months and 20 years was ca. 84 cm in both birds. Their syringes were similar-sized and looked bilaterally symmetrical as in Eurasian cranes (Rüppell, 1933). Nevertheless, the younger female produced only high-frequency calls, whereas the adult one only low-frequency calls, suggesting a lack of relations between syrinx and trachea sizes and the fundamental frequency of calls in red-crowned cranes (our unpublished data). Physiological experiments would be necessary to find out whether calls of adolescent red-crowned cranes during voice breaking are produced with one or both halves of the syrinx (e.g., Goller & Suthers, 1996; Zollinger & Suthers, 2004; Zollinger et al., 2008).

Regardless of evidence that the fundamental frequency is related primarily to the length and mass of a vibrating part of mammalian vocal folds (Titze, 1994) or avian syrengial membranes (Fee, 2002), other animals besides red-crowned crane are also able to sever the relation between the size of their sound-producing structures and the fundamental frequencies of their

vocalizations. In three free-living sciurids, the speckled ground squirrel *Spermophilus suslicus*, yellow ground squirrel *S. fulvus*, and Richardson's ground squirrel *S. richardsonii*, the fundamental frequencies of alarm calls are undistinguishable between juvenile and adult animals, in spite of a large difference in body size (Matrosova et al., 2007; Swan & Hare, 2008). In male Rocky Mountains elks *Cervus elaphus nelsoni*, the fundamental frequency of rut calls exceeds 1 kHz (Feighny et al., 2006), whereas the frequency predicted from the length of their vocal folds (3 cm) is 50 Hz (Riede & Titze, 2008). The Scottish red deer *C. e. scoticus* and Corsican deer *C. e. corsicanus* have body size and vocal fold length similar to that of the Rocky Mountains elks but produce much more lower rut calls with frequencies of 107 Hz (Reby & McComb, 2003), and 40 Hz (Kidjo et al., 2008), respectively. The sciurids, deer and cranes apparently tune their sound-producing structures to sever physical relationship between body size and fundamental frequency.

Onset and completion of voice breaking: associations with body mass gain and break-up of families

We found no relationship between voice breaking and the date of hatching, but we found an association between the onset of voice breaking and completion of body growth and achievement of adult body mass in red-crowned cranes. However, factors influencing completion of voice breaking were not identified.

In nature, juveniles start flying already at the age of 3 months (Postelnykh & Kashentseva, 2005), however they do not become self-dependent until much later, on their wintering grounds (Kamata, 1994; Archibald & Lewis, 1996). Parents take care of chicks up to the beginning of the next breeding season (Archibald & Lewis, 1996). According to observations of wild cranes, break-up of parent-chick bonds occurred from the beginning of January to mid March, i.e., when juveniles were 8–10.5 months old (Kamata, 1994).

The time of completing of voice breaking of our captive cranes coincides approximately with time of break-up of families in nature. Further data is necessary, however, to find out whether the low frequency of a chick's voice during voice breaking represents a trigger for family break-up or, conversely, the parental aggression and increasing independence of a chick results in the formation of adult voice in adolescent red-crowned cranes. Otherwise, both voice breaking and family break-ups could be triggered by a third factor or

event, e.g., by enhanced photoperiod in spring, resulting in hormonal and behavioural changes in both chicks and their parents. However, in red-crowned cranes, the proposed relationship between the hormonal secretion and voice-breaking is not so evident as in green woodhoopoes and American coots that develop their sex-specific mature ornamentation just before the completion of voice breaking (Cosens, 1981; Radford, 2004). Unlike these species, both male and female red-crowned cranes receive their adult coloration during several successive moults at the age of 2–3 years (Johnsgard, 1983; Kashentseva, 1995), i.e., approximately to the minimum reported age of first breeding (Antonyuk, 2008).

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