

Duet structure provides information about pair identity in the red-crowned crane (*Grus japonensis*)

Anna V. Klenova · Ilya A. Volodin ·
Elena V. Volodina

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Abstract We studied the acoustic features of the endangered red-crowned crane (*Grus japonensis*), and, specifically, whether or not the duets carry information about a mating pair identity. The population of this species in the wild is only approximately 2,000 individuals. In 2003–2006, we recorded 343 duets from eight captive and two wild pairs. All of the duets contained an introduction, an unordered alternation of pair mate calls, followed by the main part, representing the regular sequence of syllables, containing 1–2 male and 1–4 female calls per syllable. We subdivided the syllables into five types, by the number of male and female calls per syllable, and analyzed the occurrence of the different syllable types in the duets of the ten pairs. The analysis showed the sustainable pair-specific use of particular syllable types through the years. The discriminant analysis standard procedure, based on seven frequency and temporal parameters of male and female calls, showed 97.7% correct assignment to the pair, which is significantly higher than random values. The high pair specificity of the duet acoustic structures provides the basis for call-based censuses. This would enable the monitoring of the red-crowned crane mating pairs in their natural habitat.

Keywords Vocal behavior · Unison call · Duet structure · Call-based monitoring · Individuality · Red-crowned crane · *Grus japonensis*

Introduction

Pair duets, elaborate and often highly synchronized vocal displays, are reported for more than 220 species of 44 families (Thorpe 1972; Farabaugh 1982; Wachtmeister 2001; Hall 2004). All 15 species of the Gruidae family perform a unison call (Archibald 1976; Archibald and Lewis 1996), representing the duet by the definition of Farabaugh (1982), since “both mates participate with evident temporal coordination.” The crane duets are potentially appropriate as a non-invasive tool for call-based monitoring in nature: they are very loud and, thus, may be recorded from a distance (Terry et al. 2005). Also, the grey-crowned crane (*Balearica regulorum gibbericeps*) and the common crane (*Grus grus*) duet structures have been shown to have higher intrapair than interpair similarity, which suggests the potential for the call-based identification of nesting pairs in nature (Budde 2001; Wessling 2000).

The duet structures of cranes and, in particular, the red-crowned crane or tancho (*Grus japonensis*), the subject species of this study, were described both verbally (Masatomi and Kitagawa 1975; Vinitser 1981) and with the presentation of sonograms (Archibald 1976). However, the within- and between-pair variability in the duet structures of the red-crowned crane is still poorly understood.

The red-crowned crane is the second rarest crane species, with a total wild population of approximately 2,000 birds (Archibald 2000). It breeds on large wetlands of temperate East Asia and winters along rivers and on the

A. V. Klenova (✉) · I. A. Volodin
Department of Vertebrate Zoology, Faculty of Biology,
Lomonosov Moscow State University, Vorobiev Gory,
Moscow 119992, Russia
e-mail: klenova2002@mail.ru

I. A. Volodin · E. V. Volodina
Scientific Research Department, Moscow Zoo,
B. Gruzinskaya, 1, Moscow 123242, Russia

coastal and freshwater marshes of Japan, China, and the Korean Peninsula. There are two main breeding populations of this species: the mainland migratory population of East Asia (enveloping northeastern China and southeastern Russia) and the island sedentary population of Hokkaido Island, northern Japan (Masatomi 1981; Swengel 1996a). This species is monogamous, with stable pair bonds both within and through years (Archibald and Lewis 1996; Masatomi 2000). Pair mates jointly guard a breeding territory of 1 to 12.3 km² and share the chicks' care (Vinter 1981; Kitagawa 1982; Archibald and Lewis 1996). The observations of marked cranes of Hokkaido Island showed that they occupy the same nesting territories from year to year (Masatomi 2000). The endangered status complicates the capture and marking of the red-crowned cranes for further individual monitoring and censuses, making vocal-based monitoring of utmost importance for this species.

The red-crowned crane duet begins with the introduction (an unordered sequence of male and female calls), followed by the main part, containing a few or many regularly repeated syllables (Archibald 1976). The syllable, in its order, can contain either one or two male calls and from one to four female calls. The syllable always starts with a long and loud male call (the second male call is facultative and substantially shorter and lower in frequency than the first one). Within a syllable, the second half of the long male call is overlapped by the first female call (or sometimes with two first female calls).

The purpose of this study was to investigate the intra- and interpair variability in the duet structures of the red-crowned crane and to quantify the potential of certain duet parameters to carry information about pair identity as the background for the vocal-based monitoring of this species in nature.

Materials and methods

Subjects and study sites

We recorded duets from eight captive (nos. 1–8) and two wild (nos. 9 and 10) mating red-crowned crane pairs. The duets of pair nos. 1–5 were recorded at the Oka Crane Breeding Centre (OC) of the Oka Biosphere State Nature Reserve (Ryazan region, Russia), and pair nos. 6–8 at the Rare Bird Reintroduction Station (RS) of the Khingansky State Nature Reserve (Amur region, Russia). Pair no. 9 was recorded at Muraviovka Park for Sustainable Land Use (MP), Amur region, and pair no. 10 at Khingansky State Nature Reserve (KR). The duet recordings of pair no. 8 were courteously provided to us by RS staff. Pair nos. 1–5 were recorded from May to August in the years 2003–2006; pair nos. 6 and 7 in July to August 2005 and in May

2006; pair no. 8 between 1996 and 2000; pair no. 9 from 1 to 16 May 2006; and pair no. 10 from 19 to 26 May 2006 (Table 1).

All captive pairs, with the exception of pair no. 8, were kept in separate enclosures of about 100 m², in auditory contact with conspecifics or other crane species. Pair no. 8 was semicaptive: it lived out of the enclosure, but in proximity to humans at RS. The OC pairs could hear calls of wild common cranes, and the RS pairs could hear the calls of wild red-crowned or white-naped cranes (*Grus vipio*).

Seven of the 16 examined birds were wild-captured at various ages; the remaining nine birds were captive-raised. Pair nos. 1–5 and 8 did breed both before and throughout the study; pair no. 6 did not breed due to trauma to the female, but, since 2004, had been raising adoptive chicks (Table 1); pair no. 7 did not breed at the start of this study. Pair no. 9 had no nest, but displayed territorial behavior. Although both pair mates were unmarked, we repeatedly observed them at the same territory and never observed two pairs simultaneously, so we assume that it was the same crane pair. Pair no. 10 was nest-sitting, so, although both pair mates were unmarked, we could reliably distinguish

Table 1 Red-crowned crane pairs and the number of duet records included in the analysis: the years of birth and the number of analyzed duets per pair per year are given; *m* male; *f* female

Pair no.	Birth year	Number of analyzed duets per year				
		2003	2004	2005	2006	Total
1	m1, 1990 f1, 1993	7	4	9	20	40
2	m2, 1993 f2, 1984	7	13	13	20	53
3	m3, 1988 f3, 1985	20	20	5	20	65
4	m4, 1990 f4, 1985	19	20	10	7	56
5	m5, 1985 f5, 1986	11	7	20	20	58
6	m6, 1989 f6, 1993			20	20	40
7	m7, 2000 f7, 2000			3	10	13
8	m8, 1988 f8, 1988					7
9	m9, ? f9, ?				5	5
10	m10, ? f10, ?				6	6
Total		64	64	80	128	343

them from conspecific pairs appearing close to the nest (Table 1).

Captive pair nos. 1–7 called duets when aroused by human approach or by the capture of a chick for Zoo-technik procedures and, in 2006, also in response to playbacks of conspecific duets. We broadcasted to a focal pair no more than two playback trials per day (1–3 duets per trial), separated by silence for a minimum of 30 min. All but one captive pair called duets in response to playbacks only before or after the nest-sitting period, and did not respond during the nest-sitting. Instead, the nest-sitting pairs called duets during replacing the nest-sitting pair mate. The wild pairs shared this tendency: pair no. 9 called duets in response to playbacks, whereas pair no. 10 did not respond to playbacks but called duets during replacing a nest-sitting pair mate. The distance from the calling birds to the microphone varied from 8 to 40 m for pair nos. 1–8, from 300 to 500 m for pair no. 9, and was about 800 m for pair no. 10.

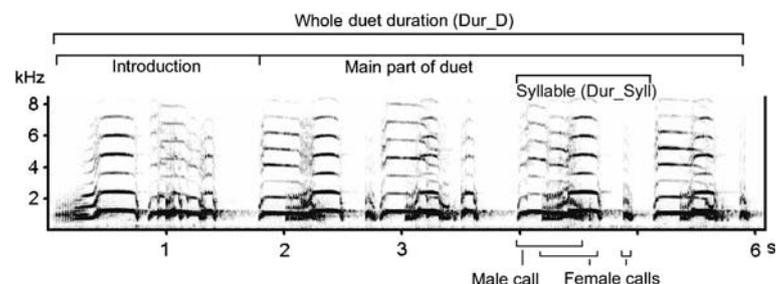
The captive birds (pair nos. 1–8) were sexed with DNA PCR analysis or by participation in breeding. The pair mates were distinctive by body constitution, coloration details, beak shape, etc., so we could distinguish between them during duetting.

The wild cranes (pair nos. 9–10) were not sexed. However, the male and female patterns in the red-crowned crane duets are clearly distinctive (Archibald 1976), so we could reliably distinguish between the calls of each sex based exclusively on duet spectrograms (Fig. 1).

Acoustic records and analyses

For recording sounds, we used a Marantz PMD-222 (D&M Professional, Kanagawa, Japan) cassette recorder with a Sennheiser K6-ME67 (Sennheiser Electronic, Wedemark, Germany) shotgun condenser microphone. For playback, we used the Marantz PMD-222 with a Creative Travel-Sound 400 dynamic (Creative Labs., Dublin, Ireland). Both call digitizing (22.05-kHz sampling rate, 16-bit precision) and measurements were made with Avisoft SASLab Pro v.4.3 software (Avisoft Bioacoustics, Berlin, Germany).

Fig. 1 Spectrogram of the red-crowned crane duet, consisting of the introduction and main part with four syllables. In the given duet, all syllables contain one male and two female calls. Two measured parameters, *Dur_D* a whole duet duration and *Dur_Syll* a syllable duration, are also shown



Then, we made a low-pass filtration at 6 kHz and sampling frequency conversion to 11.025 kHz. Spectrograms were created with a Hamming window, FFT-length 512 points, frame 50%, and overlap 96.87%, providing a time resolution of 1.5 ms and a frequency resolution of 21 Hz.

We classified syllables within the main parts of the duets into five types, by the proportion of male and female calls within a syllable (Fig. 2): S1_1, with one male and one female call (Fig. 2a); S1_2, with one male and two female calls (Fig. 2b); S1_3, with one male and three female calls (Fig. 2c); S1_4, with one male and four female calls (Fig. 2d); and S2_x, with two male and from one to four female calls (Fig. 2e).

We prepared three different samples of duets: the first one to estimate the proportion of different syllable types for each pair, the second one to estimate the percentages of different syllable types for each pair between years, and the third one to estimate the temporal frequency variability of calls within syllables of the most widespread types S1_2 and S1_3.

To estimate the interpair variability in the occurrence of different syllable types, we assigned syllables to a certain syllable type visually by spectrogram, taking from 5 to 65 duets per pair (Table 1). In total, we analyzed the syllable types and percentages of their occurrence for 343 duets.

To analyze the percentages of different syllable types between years, we used 4–20 duets per pair per year from pair nos. 1–6, taking into account 312 duets in total (Table 1).

To analyze the temporal and frequency call parameters within syllables, we selected only whole (recorded from the beginning to the end) duets of good quality (with high signal-to-noise ratios and those not superimposed with background noise and vocalizations of other birds). We took 7, 5, and 6 duets per pair respectively for pair nos. 8, 9, and 10, and 10 duets per pair for pair nos. 1–7 with an equal number of duets per year, giving 88 duets in total. Within these duets, we measured the call parameters only for the most widespread syllable types, S1_2 and S1_3 (omitting other syllable types occurring in the duets). If less than 14 syllables of types S1_2 and S1_3 were presented in the given duet, we measured all of them; for duets

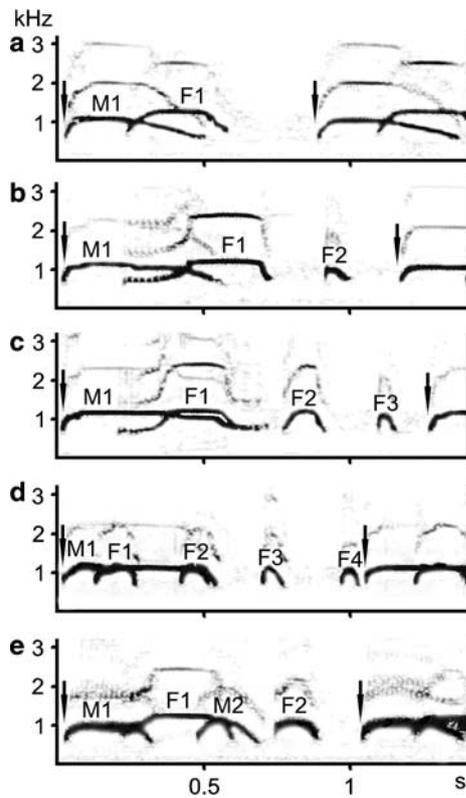


Fig. 2a–e Spectrograms illustrating the five syllable types, classified within the main parts of the red-crowned crane duets. *M1* and *M2* male calls; *F1*, *F2*, *F3*, and *F4* female calls. The *arrows* point to the start of a syllable. **a** Syllable S1_1, containing one male and one female call (pair no. 1). **b** Syllable S1_2, containing one male and two female calls (pair no. 4). **c** Syllable S1_3, containing one male and three female calls (pair no. 4). **d** Syllable S1_4, containing one male and four female calls (pair no. 9). **e** Syllable S2_x, containing two male and from one to four female calls (pair no. 2)

with more than 14 syllables of these two types, we measured the first 14 in order, counting from the beginning of the duet. For each syllable, we measured seven parameters (Fig. 3): *Dur_Syll*—syllable duration, i.e., the duration from the beginning of the male call of the given syllable to the beginning of the male call of the next syllable, *Dur_M*—the male call duration, *Dur_F1*—the first female call duration, *Dur_F2*—the second female call duration, *Fmax_M*—the male call maximum fundamental frequency, *Fmax_F1*—the first female call maximum fundamental frequency, *Fmax_F2*—the second female call maximum fundamental frequency. All of the measurements were made with a reticule cursor in the spectrogram window of Avisoft and exported automatically to Excel[®] (Microsoft Corporation).

Then, we calculated the mean values of the syllable call parameters within each duet and measured the whole duration for each duet (*Dur_D*) (Fig. 1). For each duet, we measured eight parameters: seven mean values for the

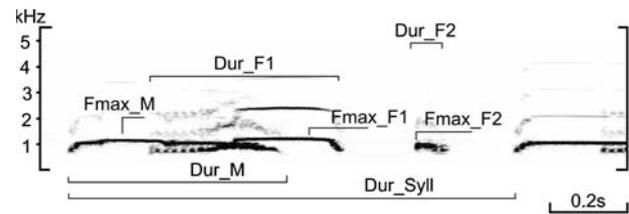


Fig. 3 The measured parameters of calls within syllables of red-crowned crane duets. *Dur_Syll* syllable duration, *Dur_M* male call duration, *Dur_F1* first female call duration, *Dur_F2* second female call duration, *Fmax_M* male call maximum fundamental frequency, *Fmax_F1* first female call maximum fundamental frequency, *Fmax_F2* second female call maximum fundamental frequency

temporal and frequency parameters of the within-syllable calls and the whole duration of a duet. All of the duet parameters could be easily extracted from both duets recorded from a distance of 8–40 m in captivity and from duets recorded from distances of 300–800 m in the field (compare, e.g., Fig. 2a, d).

Statistics

We used the Wilcoxon matched pairs *T* test to compare the male and female call parameters within duets. We performed one-way ANOVA, with “pair” as the grouping variable, to compare the variability of eight duet parameters within and between pairs. Then, we used the discriminant analysis standard procedure based on seven duet parameters to determine whether duets could be assigned to the correct pair. To validate discriminant analysis results, we performed a randomization analysis (Solow 1990). To perform the randomization analysis, 500 permutation procedures with software macros, specially created by A.A. Lisovsky for STATISTICA software, were used. Each permutation procedure included the random permutation of 88 duets among ten randomization groups, according to the number of pairs examined and followed by the discriminant analysis standard procedure. We then created the distribution of mean duet classification percentages to randomization groups and estimated a position of the observed value of assignment to pairs within this distribution. If the observed value exceeded 95% of values within this distribution, we established that the observed value did differ significantly from the random observation with probability $P < 0.05$; and if the observed value exceeded 99% of values within this distribution, we established that the observed value did differ significantly from the random observation with probability $P < 0.01$ (Solow 1990). All of the statistical analyses were carried out in STATISTICA v. 6.0 (StatSoft, Inc., Tulsa, OK, USA).

Results

Duet structure

The red-crowned crane duet represents a sequence of partially overlapped tonal male and female calls, i.e., according to Farabaugh (1982), it is a simultaneous duet. Both males and females may start a duet with the production of a start call. Of the 174 duets examined, 55 (32%) were male-started and 119 (68%) were female-started (Table 2). However, these data are biased toward pairs producing mostly female-started duets. In two of the six pairs that contributed the most to the duet samples, nearly all duets were female-started. After two pairs from the duet sample were excluded, the percentage of female-started duets decreased to 51.4%. At the same time, the data on duet starting suggest high interpair variability. In three pairs, all or nearly all of the duets were female-started; in one pair, all duets were male-started; and in the remaining five pairs, a female or a male started the duet with equal probability (Table 2).

Usually, the female calls are long at the beginning of the introduction and shorten progressively to the beginning of the main part. On the contrary, the male calls are short at the beginning of the introduction and become longer throughout a duet. With female calls becoming shorter and the male calls becoming longer during an introduction, it results in the disordered alternation of pair mate calls. The main part of the duets looked much more regular and could be easily subdivided into syllables, which always began with a long male call (Fig. 1). A syllable could contain from one to four female calls per long male call (Fig. 2). The total duration of the introduction varied from 0.73 to 2.09 s (mean ± SD = 1.34 ± 0.29 s, *n* = 88), and the total duration of the main part from 4.28 to 42.73 s (mean ± SD = 18.52 ± 9.51 s, *n* = 88).

Table 2 Numbers of duets per pair, started by either male or by female, for the nine red-crowned crane pairs examined

Pair no.	Duets started by male	Duets started by female	<i>N</i>
1	9	7	16
2	0	21	21
3	19	20	39
4	2	42	44
5	6	12	18
6	11	10	21
7	2	5	7
8	6	0	6
9	0	2	2
Total	55	119	174

N number of duets analyzed per pair

During this four-year study, we have never heard a male or a female solo: all pair mates called only together while standing within 1–5 m of each other and performing complex visual displays, described in detail by Masatomi and Kitagawa (1975). The duets of red-crowned cranes are very loud, and in the moist windless weather on the plains of KR, we heard them from distances of up to 1.5 km.

Quantitative analysis of the temporal and frequency parameters of the duets

ANOVA showed highly significant interpair differences for all of the frequency and temporal parameters of the within-syllable calls and in the whole duet duration (Table 3). We found that Fmax_F1 and Dur_M were the most pair-specific parameters, whereas Dur_D was the least pair-specific parameter.

Discriminant analysis standard procedure with the seven frequency and temporal parameters of the male and female within-syllable calls included in the analysis (without Dur_D, excluded by ANOVA as the least pair-specific), showed 97.7% correct assignment to the pairs, which is significantly higher (*P* < 0.01) than the random value (mean ± SD = 22.1 ± 5.4), calculated with randomization. Only two duets of 88 (one from captive pair no. 2 and another from wild pair no. 10) were misclassified. Three parameters, in order of decreasing importance, contributed the most in discrimination: Fmax_F1; Fmax_M, and Dur_M.

Temporal characteristics of duets

For the total sample, Dur_M for syllables within the main duet part was 458 ± 82 ms, Dur_F1 was nearly two times shorter at 240 ± 75 ms, and Dur_F2 was shorter still at 115 ± 28 ms (Wilcoxon matched pairs test, *n* = 88, *T* = 0, *Z* = 8.15, *P* < 0.001 for all comparisons). Within the pairs, the data were consistent with those received for the total duet sample: the Dur_M did exceed the Dur_F1, and the Dur_F1 did exceed the Dur_F2 (Table 3). We suppose that such a ratio of male and female call durations within syllables represents a species-specific rather than a pair-specific characteristic.

Frequency characteristics of duets

For the total duet sample, Fmax_M = 1.05 ± 0.07 kHz was significantly lower than Fmax_F1 = 1.18 ± 0.11 kHz (Wilcoxon matched pairs test, *n* = 88, *T* = 278, *Z* = 6.99, *P* < 0.001). Fmax_F2 = 1.05 ± 0.13 kHz did not differ

Table 3 ANOVA results for the interpair differences and values of temporal and frequency parameters (mean \pm SD) of male and female calls produced within syllables, constituting the main part of a duet, in the ten examined red-crowned crane pairs

Pair no.	Dur_D (s)	Dur_Syll (ms)	Dur_M (ms)	Dur_F1 (ms)	Dur_F2 (ms)	Fmax_M (kHz)	Fmax_F1 (kHz)	Fmax_F2 (kHz)	N
1	22.6 \pm 11.7	1,057 \pm 50	486 \pm 31	277 \pm 20	125 \pm 22	0.91 \pm 0.02	1.14 \pm 0.04	1.0 \pm 0.04	10
2	11.4 \pm 2.7	892 \pm 41	397 \pm 26	222 \pm 22	93 \pm 10	1.06 \pm 0.04	1.16 \pm 0.03	0.94 \pm 0.04	10
3	27.1 \pm 10.7	879 \pm 47	439 \pm 35	215 \pm 29	78 \pm 19	1.04 \pm 0.03	1.19 \pm 0.04	0.92 \pm 0.06	10
4	17.0 \pm 5.9	1,355 \pm 81	589 \pm 26	418 \pm 47	152 \pm 18	1.08 \pm 0.03	1.17 \pm 0.01	1.14 \pm 0.02	10
5	20.2 \pm 8.9	954 \pm 54	399 \pm 18	233 \pm 39	104 \pm 15	1.06 \pm 0.01	0.99 \pm 0.01	0.92 \pm 0.03	10
6	27.4 \pm 9.4	921 \pm 56	382 \pm 11	170 \pm 15	109 \pm 20	1.13 \pm 0.02	1.18 \pm 0.02	1.10 \pm 0.05	10
7	17.6 \pm 8.0	1,129 \pm 90	591 \pm 38	214 \pm 15	150 \pm 10	1.06 \pm 0.04	1.39 \pm 0.03	1.31 \pm 0.03	10
8	13.6 \pm 2.6	880 \pm 39	411 \pm 15	226 \pm 22	104 \pm 9	0.99 \pm 0.02	1.27 \pm 0.01	1.06 \pm 0.07	7
9	14.5 \pm 5.0	965 \pm 36	449 \pm 15	181 \pm 22	121 \pm 10	1.11 \pm 0.01	1.09 \pm 0.01	1.04 \pm 0.01	5
10	24.5 \pm 9.0	946 \pm 34	393 \pm 21	192 \pm 14	108 \pm 21	1.09 \pm 0.02	1.16 \pm 0.03	1.09 \pm 0.03	6
Total	19.9 \pm 9.5	1,006 \pm 159	458 \pm 82	240 \pm 75	115 \pm 28	1.05 \pm 0.07	1.18 \pm 0.11	1.05 \pm 0.13	88
F-ratio	4.2	62.9	86.3	62.6	20.0	43.6	144.4	79.7	
	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$	

Dur_D whole duet duration, *Dur_Syll* syllable duration, *Dur_M* male call duration, *Dur_F1* first female call duration, *Dur_F2* second female call duration, *Fmax_M* male call maximum fundamental frequency, *Fmax_F1* first female call maximum fundamental frequency, *Fmax_F2* second female call maximum fundamental frequency, *N* the number of duets

significantly from *Fmax_M* ($T = 1,740$, $Z = 0.56$, $P = 0.57$). However, strong interpair differences were observed in *Fmax_M* and *Fmax_F1* (Fig. 4). In all 15 duets of pair nos. 5 and 9, the *Fmax_M* was significantly higher than the *Fmax_F1* (Wilcoxon matched pairs test, $n = 15$, $T = 0$, $Z = 3.4$, $P < 0.001$), whereas in all 73 duets of the remaining eight pairs, the *Fmax_M* was significantly lower than the *Fmax_F1* (Wilcoxon matched pairs test, $n = 73$, $T = 0$, $Z = 7.42$, $P < 0.001$).

Percentages of different syllable types occurring in the duets of each pair within and between years

The percentages of different syllable types showed clear interpair differences. The syllable S1_2 was the most widespread in the duets of the red-crowned crane, being over 60% of all syllables (Fig. 5), whereas S1_1 = 19.4%, S1_3 = 11.7%, S1_4 = 0.8%, and S2_x = 7.6%. However, whereas pair nos. 1, 2, 5, 6, 8, and 10 produced primarily syllable S1_2 (over 70%), pair nos. 4, 7, and 9 had 36.8%, 71.9%, and 60.3%, respectively, primarily produced syllable S1_3 and used syllable S1_4 (the other seven pairs lacked this syllable type), and pair no. 3 produced 54.8% of syllable S1_1 and no S1_3 or S1_4 syllables.

The comparison between several successive years for pair nos. 1–6 showed that each pair maintained high rates of particular syllable types both within and between all of the four study years (Table 4). For example, pair no. 3 produced not less than 42.2% of the S1_1 syllable, pair no. 4 produced between 30.6% and 46.8% of the S1_3 syllable, pair no. 2 between 17.3% and 25% of the S2_x

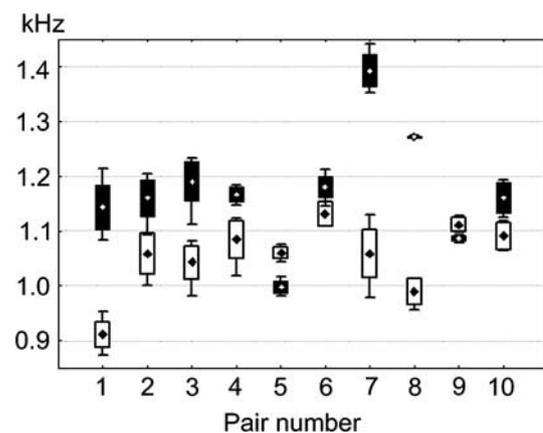


Fig. 4 Values of the male call maximum fundamental frequency (black central points, white boxes) and values of a first female call maximum fundamental frequency (white central points, black boxes) in the syllables of duets for the ten red-crowned crane pairs examined. The central points show mean values, the boxes represent the SD, and the whiskers the minimum and maximum values

syllable, pair no. 4 between 16.1% and 24.3% of the S2_x syllable, and pair nos. 1, 2, 5, and 6 not less than 62.5% of the S1_2 syllable.

Discussion

We revealed numerous interpair differences in the duet structure of the examined ten pairs of red-crowned crane. The pairs did differ in the preferences of particular syllable types and maintained their preferences throughout the years (Fig. 5, Table 4). The pairs also differed by the sex of

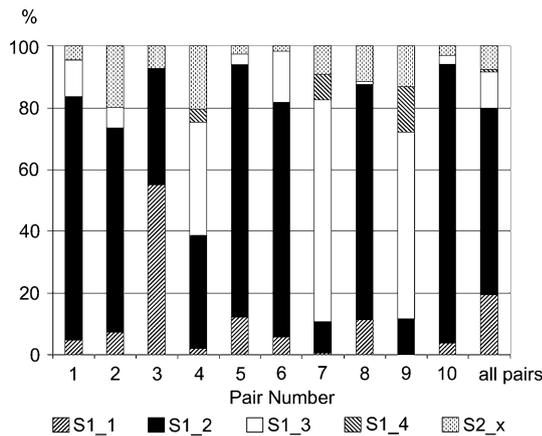


Fig. 5 Percentages of the five syllable types occurring within duets from the examined red-crowned crane pairs and for the total sample of the ten pairs. *S1_1* syllable type containing one male and one female call. *S1_2* syllable type containing one male and two female calls. *S1_3* syllable type containing one male and three female calls. *S1_4* syllable type containing one male and four female calls. *S2_x* syllable type containing two male and from one to four female calls

a caller starting the duet: in some pairs, the mate of either sex started the duet, whereas in others, only the male or only the female started the duet (Table 2). The pairs also differed by the ratio of maximum call frequencies in the first male and the first female calls within syllables. In eight out of ten pairs, the male called lower than the female, whereas in the other two pairs, the female called lower than the male.

The listed set of characteristics was already sufficient to distinguish between the duets of neighbor pairs with a fair degree of confidence, thus, enabling the monitoring of a certain pair by its duets throughout the years. The monitoring can be based on the visual analysis of spectrograms and does not require expensive equipment or staff training, proving its value for conservation research in the field (Wessling 2000; Terry et al. 2005).

Furthermore, the discriminant analysis, based on measured temporal and frequency syllable parameters, provides a high reliability of discrimination between the calling pairs. Therefore, qualitative and quantitative methods of identification complement each other and, taken together, can enhance the reliability of call-based monitoring for red-crowned crane pairs.

Individual specificity in call characteristics was reported for many bird species (for a review, see Falls 1982), whereas pair specificity is reported for a small number of species. Besides the grey-crowned and common cranes (Budde 2001; Wessling 2000), the interpair differences were also found in the male duet parts of the Steere’s liocichla (*Liocichla steerii*) (Mays et al. 2006). For the Australian magpie-lark (*Grallina cyanoleuca*), the interpair differences in the male and female preferences of particular vocal types have also been identified (Hall 2006).

Furthermore, pairs of the Australian magpie-lark responded differently to the duets of neighbor and unfamiliar conspecific pairs (Hall 2000).

A special point for discussion is the remarkable reversion of maximum call frequencies in the first male and first female calls within syllables in two of the ten examined pairs. These data are only partially consistent with other evidence on the ratios of fundamental frequencies in male and female crane calls. For example, Archibald (1976) suggests that, in 14 crane species, the female duet calls were always higher in fundamental frequency than the male calls. Similarly, for the whooping crane *Grus americana*, Carlson and Trost (1992) reported significantly lower fundamental frequencies for the male guard call (only 85% of the female guard call fundamental frequency).

For the red-crowned crane, Archibald (1976) reported the mean ± SD values for the male call maximum fundamental frequency of 1.03 ± 0.02 kHz and those for the female call of 1.19 ± 0.16 kHz. On the whole, our data for the total duet sample are in good accordance with those of Archibald (1976): the mean ± SD for the male call maximum fundamental frequency was 1.05 ± 0.07 kHz, whereas for the female first syllable call, it was 1.18 ± 0.11 kHz (Table 3). At the same time, in two pairs (nos. 5 and 9), the first female call fundamental frequency was significantly lower than that of the male call (Table 3).

As a rule, the lower call frequency is considered to be related to the larger size/weight in one of the sexes. Whereas the male and female red-crowned cranes are practically indistinguishable both by overall appearance and by behavior, the males are usually larger than the females: the reported mean ± SD body weight values are 10.01 ± 0.94 kg (*n* = 9) for adult males and 8.57 ± 0.66 kg (*n* = 10) for adult females (Postelnykh and Kashentseva 2005). These data are consistent with Swengel (1996b) reporting that, in many other crane species, the males are larger than the females. Our data showed, however, that the lower frequencies were not strictly related to the larger weights of the pair mates. In pair no. 5, the male call frequency was higher, in spite of the fact that, at the beginning of 2005, this male weighed 9 kg, whereas the female of this pair weighed only 8.6 kg. At the same time though in pair no. 4, the male call frequency was lower, the male weighed only 9 kg, whereas the female weighed 10.1 kg (T. Kashentseva, personal communication).

These findings are interesting in relation to an enough representative body of data showing intersexual difference in call frequencies as coming from the differences in sizes between sexes, related to the sizes of their vocal apparatus (Miller 1934; Ballintijn and ten Cate 1997). Consistently, for the larger-sized males, the correspondingly lower fundamental frequencies were found in the common

Table 4 Percentages of occurrence within year in the duets of different syllable types for six red-crowned crane pairs

Pair no.	Year	S1_1	S1_2	S1_3	S1_4	S2_x	N
1	2003	3.4	88.1	8.5	0	0	7
	2004	7.7	75	15.4	0	1.9	4
	2005	9.4	83	5.8	0	2.8	9
	2006	3.7	77.5	13.1	0	5.7	20
2	2003	11.8	63.2	0	0	25	7
	2004	6.3	69.6	4.6	0	20.5	13
	2005	10.2	71.4	1.1	0	17.3	13
	2006	5.1	63.4	12.5	0	19	20
3	2003	57.6	31.9	0	0	10.5	20
	2004	42.2	50.3	0	0	7.5	20
	2005	72	24.6	0	0	3.4	5
	2006	56.8	38.6	0	0	4.6	20
4	2003	0	32.6	41.4	3.7	24.3	19
	2004	4.4	46.7	30.6	2.2	16.1	20
	2005	3.1	46.9	31.3	0	18.8	10
	2006	0	14.5	46.8	14.5	24.2	7
5	2003	12.7	81.5	2.9	0	2.9	11
	2004	14.1	73.1	5.1	0	7.7	7
	2005	13.3	80	4	0	2.7	20
	2006	11.2	84.2	2.9	0	1.7	20
6	2005	1.4	62.5	33.3	0	2.8	20
	2006	8.4	83	5.7	0	0.9	20

N number of duets

screech-owl *Otus asio* (Cavanagh and Ritchison 1987), black-necked grebe *Podiceps nigricollis* (Nuechterlein and Buitron 1992), collared dove *Streptopelia decaocto* (Ballintijn and ten Cate 1997), orange-billed fruit dove *Ptilinopus iozonus* (Baptista and Gaunt 1997), marbled frogmouth *Podargus ocellatus* (Smith and Jones 1997), and parrots *Poicephalus* spp. (Venuto et al. 2001). Otherwise, for the larger-sized females, the correspondingly lower fundamental frequencies were found in the white-tailed hawk *Buteo albicaudatus* (Farquhar 1993) and Leach's storm-petrel *Oceanodroma leucorhoa* (Taoka et al. 1989).

For the red-crowned crane, we showed that the differences in call frequencies between sexes did not directly follow the weight/size differences between sexes. We also found that the pair mates of this species could not be sexed reliably by only fundamental frequencies of calls within duets. Further research is necessary, however, to compare male and female fundamental frequencies of calls other than duets.

On the other hand, the sex of duetting red-crowned cranes could be reliably determined by calling rate. Since a female produced more calls than a male in the most often occurring syllable types, the female calling rate was evidently higher (Fig. 5). Another sex-specific feature was the

duration of calls within syllables, with the male call always being longer than the first female call.

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