



Long-term stability in the vocal duets of the endangered Siberian Crane *Leucogeranus leucogeranus*

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Abstract

Vocal-based monitoring is increasingly being used as a non-invasive method for identifying individuals within avian populations and is promising for the Siberian Crane, *Leucogeranus leucogeranus*. This is a poorly studied, long-lived, secretive and critically endangered bird species that breeds in the Arctic tundra of western and eastern regions of Siberia. We assessed between- and within-year stability of individual-specific vocal features in duets of Siberian Crane and tested the effect of pair-mate change on their stability. Previous findings showed that duets are specific to different pairs of birds; however, it is still unknown how long pair-specific traits of duets remain and if they change in the course of a year or when birds re-mate. We recorded duets of 15 reproductively active pairs in the Oka Crane Breeding Centre in 2003–2006 and 2013–2017. We found that pair-specific vocal signatures remained stable both within the year and across ~10 years. After a change of mate, most of the variables we measured in the call did not change in any of the birds. Our data suggest that the stability of the individually specific vocal features may enable Siberian Cranes to be reliably identified by their duets over the birds' lifetime. We believe that our work can increase confidence in the use of acoustic recognition techniques for endangered crane monitoring programs. Our results also suggest that Siberian Cranes may use their duets to form long-term social bonds between neighbours.

Keywords Vocal plasticity · Call-based monitoring · Voiceprinting · Individuality · Ageing · Season variability

Introduction

An important question in animal communication is for how long individually distinctive signals like calls are stable. The answer has important implication for understanding the social structure and dynamics. Most studies have

documented acoustic individuality over only short time spans (Falls 1982; Charrier et al. 2001; Mathevon et al. 2003; Cure et al. 2009 etc.). A few studies have addressed long-term individuality in calls of birds and mammals without vocal learning and have failed to find it in many cases (birds: Eakle et al. 1989; Guyomarc'h et al. 1998; Puglisi and Adamo 2004; Walcott et al. 2006; Volodin et al. 2008; Cornec et al. 2015, mammals: Jorgensen and French 1998; Snowden and Elowson 1999; Rukstalis et al. 2003; Chulkina et al. 2006; Matrosova et al. 2009, 2010). Calls may vary in relation to various factors in different long-lived animal species. For example, vocalizations can change with age (birds: Kipper and Kiefer 2010; mammals: Reby and McComb 2003; Fischer et al. 2004; Charlton et al. 2009; Mathevon et al. 2010) or season of the year (Nottebohm et al. 1986, 1987; Smith et al. 1997; Ritters et al. 2000; Kunc et al. 2007; Voigt and Leitner 2008). Temporal variation in social or environmental factors could underlie changes in calls of species with vocal learning (e.g. Nowicki 1989; Hile et al. 2000) or that lack learning (Snowden and Elowson 1999; Rukstalis et al. 2003; Walcott et al. 2006). However, for bird species

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that lack vocal learning, effects of age, season or social factors have not been investigated adequately (Walcott et al. 2006; Klenova et al. 2012).

Knowledge of the consistency of vocal individuality over time also has practical significance. To be used as a long-term monitoring tool, vocalizations must have two attributes: (1) high between-individual differences, and (2) temporal stability (Terry et al. 2005). A few studies that used individually marked animals suggest that some species have vocalizations that are individually specific over multiple years; this observation suggests that the same individuals may be identifiable over long time periods (Lengagne 2001; Laiolo et al. 2007; Klenova et al. 2009, 2012; Kirschel et al. 2011; Petruskova et al. 2016). At the same time, it is known that many species lack temporally stable vocal features that code individuality (e.g. Eakle et al. 1989; Snowdon and Elowson 1999; Rukstalis et al. 2003; Puglisi and Adamo 2004; Walcott et al. 2006; Volodin et al. 2008; Matrosova et al. 2009, 2010; Cornec et al. 2015; Humphries et al. 2016). Therefore, before planning any long-term vocal monitoring projects, we should check vocalizations of each new species not only for existence of strong individually specific traits, but also for their long-term stability.

Cranes (Gruidae) are good models to study the relationships of age, season and social factors to vocal individuality, since they are long-lived, territorial, highly vocally active birds without obvious vocal learning (Archibald 1976; Flint 1987; Archibald and Lewis 1996; Meine and Archibald 1996). Acoustic monitoring is promising for cranes and could be very useful for conservation of the Siberian Crane *Leucogeranus leucogeranus*, as this species has Critically Endangered status in the IUCN Red List (<https://www.iucnredlist.org>) and its wild population is estimated to be about 4000 birds (Li et al. 2012). Like other crane species, the Siberian Crane is monogamous and pair bonds may last a long time (Sauey 1985; Flint 1987; Archibald and Lewis 1996; Meine and Archibald 1996; Degtyarev and Labutin 1999; Germogenov et al. 2009). Nevertheless, divorces occur in all crane species (Littlefield 1981; Nesbitt 1989; Hayes 2005; Henne and Blahy-Henne 2013). Crane pairs perform vocal duets throughout most of the year. These are a temporally coordinated succession of pair-mate calls and occur in all crane species (Archibald 1976; Archibald and Lewis 1996). Pair-specific traits in duets have been already reported for several crane species (Wessling 2000; Budde 2001; Klenova et al. 2008; Bragina and Beme 2010; Policht and Tichackova 2010). Previous studies also showed that pair-specific characteristics of duets are stable over at least several successive years in at least three crane species, namely, the Red-crowned *Grus japonensis*, Siberian Crane, and Common Crane *Grus grus* (Klenova et al. 2009; Bragina 2008; Policht and Tichackova 2010). However, cranes can live and stay reproductively active for up to 70 years

(Archibald and Lewis 1996), so information over longer periods of observation is needed to report about the vocal stability over a more meaningful portion of the birds' entire lifespans. Vocal variability of individual birds around the year also has not been investigated for any crane species. Finally, it is not known what happens to the duet part of a single bird when a crane re-mates with a different bird due to divorce or its partner's death. So in this study, we examined vocal stability of Siberian Crane duets both within and across years (over the ~ 10 year period) and also analysed the influence of pair-mate changes on it.

Methods

Study site and animals

Our subjects were 27 Siberian Cranes that formed 15 breeding pairs in 2003–2017 (Table 1). The cranes were kept in the Crane Breeding Centre of Oka Biosphere State Nature Reserve (Ryazan region, Russia). Each pair was kept in a separate enclosure of about 100 m² in auditory contact with other cranes. Two of the 27 birds were wild-captured, and the others were raised in captivity. Cranes were 3 to 26 years of age when first recorded.

Acoustic recordings

We recorded Siberian Crane duets in May–July 2003, 2004 and March–November 2013, 2015; additional recordings of newly formed pairs were made in 2006 and 2017. During each year, we recorded each pair repeatedly, for 4–20 days (1–4 duets per day). We used three independent call samples for the different analyses and analysed 476 duets in total.

With the first sample, we estimated intra-pair vocal stability of duets over the ~ 10 year period. This sample included duets of 10 pairs (pairs #1–7, 9, 10 and 12) that remained together for at least 7 years. We recorded them twice: in 2003, 2004 or 2006 and again in 2013 or 2015 (with intervals of 7–11 years; mean 9.9 years; Table 1). We included in analysis only duets recorded in April–July and used 219 duets (16 to 24 duets per pair, 4 to 12 duets per pair per year, mean 11 duets per pair per year; Table 1).

With the second sample, we estimated intra-pair vocal stability of duets within years. This sample included duets of 11 Siberian Crane pairs (pairs #1–7, 9, 12, 14, 15). We recorded them at least during three seasons of the year (in March–April, June–July and September–November) in 2013 or 2015, at intervals of 2–3 months (Table 1). For the sample we used 329 duets (13 to 35 duets per pair, 4 to 12 duets per pair per season, mean 10 duets per pair per season; Table 1).

Three cranes died from natural causes during our study (two males from pairs #8 and 12, and female from pair

Table 1 The Siberian Crane (*Leucogeranus leucogeranus*) pairs and analysed duets

Pair no	Bird's name and year of birth	Number of analysed duets per year						
		2003	2004	2006	2013	2015	2017	Total
1	m1—Sergey—1980 f1—Banyl—1986		12			12 (11/12/12)		47
2	m2—Kunovat—1987 f2—Walsrode—1991		12			12 (11/12/12)		47
3	m3—Kieng—1986 f3—Glas—1994		12			12 (9/12/12)		45
4	m4—Kolyma—1982 f4—Bilipu—1992		7			12 (10/7/5)		29
5	m5—Nazar—1980 f5—Julia—1981		12			12 (11/9/12)		44
6	m6—Bardye—1996 f6—Bur—1996	12			12 (11/12/12)			47
7	m7—Uchur—1978 f7—Samgym—1996		10		12 (12/10/12)			44
8	m8—Svet—1980 f8—Agidel—1989*	12						12
9	m9—Chara—2003 f8—Agidel—1989*			9	9 (5/4/4)			22
10	m10—Granat—2001* f9—Mirande—1997		12		4			16
11	m10—Granat—2001* f10—Lena—2012					9		9
12	m11—Bakul—1986 f11—Buguchen—1986*		12		12 (7/12/12)			43
13	m12—Taz—2012 f11—Buguchen—1986*						12	12
15	m14—Tiung—2003 f13—Soima—2003					(12/12/6)		30
14	m13—Uchta—2005 f12—Kama—2003					(7/10/12)		29

The years of birth, names of the birds and the number of the analysed duets per pair are given. The duets without the brackets are those we used to compare the duets between years (first duet sample) or before and after re-mate (third duet sample); the duets in brackets (recorded in spring/summer/autumn) are those we used for the analysis of seasonal variation (second duet sample)

m male, f female

*Birds that were recorded with different mates during the study period

#10) in 2003, 2015 and 2013, respectively. Their pair-mates were placed with young birds and successfully formed new pairs during the same or next year. Thus, in 2006, 2015 and 2017 we were able to record pairs #9, 11 and 13, that include one of the pair-mates from pairs #8, 10 and 12, respectively. So, with the third sample, we estimated effects of pair-mate change on the vocal stability of duets. For this, we used 30 duets (9 to 12 duets per pair) from these three newly formed pairs (pairs #9, 11 and 13) and compared them with 28 duets (4 to 12 duets per pair) of the former pairs (pairs #8, 10 and 12). For the third

sample we used 58 duets; duet recordings from former and new pairs were made at intervals of 2–4 years (Table 1).

Most of the duets we recorded were produced in response to human approach to the enclosure or during routine daily care. The pair-mates called while standing close one another; the distance from birds to the microphone was 5 to 40 m. We distinguished between the duetting male and female by coloured led bands and external features.

We used a Marantz PMD-222 analogue tape recorder (DandM Professional, Kanagawa, Japan) with Type II chrome audiocassette EMTEC-CS II (EMTEC Consumer

Media Ludwigshafen, Germany) and a shotgun condenser Sennheiser K6-ME67 microphone (Sennheiser electronic, Wedemark, Germany) during 2003–2006; or a Marantz PMD-660 CF recorder (48 kHz, 16 bit) with AKG C1000S microphone (AKG Acoustics GmbH, Vienna, Austria) during 2013–2017. These systems provided high-quality recordings within ranges 40–14,000 Hz and 40–24,000 Hz, respectively. The variation in recording equipment could not influence duet variables, measured in this study, since we used only the most stable for propagation acoustic variables for analyses, like temporal and fundamental frequency characteristics, and did not use any characteristics or power spectrum (see below).

Acoustic analysis

We digitized analog recordings at a 48-kHz sampling rate and analysed digital recordings with Avisoft SASLabPro v.5.1.23 (Avisoft Bioacoustics, Berlin, Germany). We down-sampled crane duets from 48 to 11 kHz with simultaneous anti-aliasing filtration and created spectrograms with a 1024-point Hamming window, frame 50%, overlap 96.87%, providing time resolution of 2.9 ms and frequency resolution of 11 Hz. We chose for analysis only duets of good quality, that were not masked with any background noise and were recorded directly (i.e. without any barrier between birds and the microphone). All measurements were made manually from screen in the Avisoft spectrogram window with the reticule cursors and exported automatically to Microsoft Excel (Microsoft Corp., Redmond, WA, USA).

Duets begin with the introduction (1–3 long calls of a male and a female), followed by the main part, where partners commence to call in turn with variable overlap (Bragina and Beme 2010; Fig. 1a). Female calls are higher in fundamental frequency than male calls (Bragina and Beme 2010), so it was easy to distinguish calls of the two sexes in analysis of spectrograms. For each duet we measured total duration (to ± 2.9 ms precision; *Dur_duet*). Then we randomly selected two syllables from the first half and two from the second half of the duet. For each syllable, we measured 11 variables (temporal variables to ± 2.9 ms, frequency variables to ± 11 Hz; Fig. 1b): *Dur_Syll*—syllable duration, i.e. the duration from the beginning of a given male call to the beginning of the next male call; *Dur_M*—duration of the male call, *Dur_F*—duration of the female call; *Dur_FF*—duration from the beginning of the given female call to the beginning of the next female call; *Dur_MF*—the duration from the beginning of the given male call to the beginning of the next female call; *Fmax_M*, *Fmin_M*, *Fpeak_M*—maximum, minimum and peak fundamental frequencies of the male call; *Fmax_F*, *Fmin_F*, *Fpeak_F*—maximum, minimum and peak fundamental frequencies of the female call. For these 11 variables we then calculated mean values

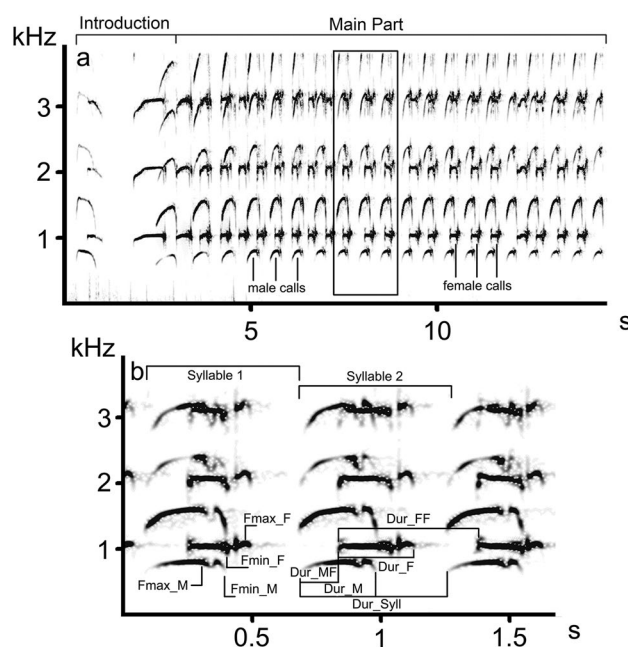


Fig. 1 **a** Spectrogram of a Siberian Crane's (*Leucogeranus leucogeranus*) complete duet. The introduction, main part, and male and female calls are shown. **b** Enlarged section of a duet fragment marked on the upper figure shows three subsequent syllables and the measured time–frequency variables

for the four syllables chosen for the analysis. Thus, each duet was presented by 11 mean values of temporal and frequency syllable variables and one measurement of a whole duet duration.

Statistical analyses

Distribution of residuals for all measured variables did not differ from normality assumption for each pair ($p > 0.05$, Kolmogorov–Smirnov test). For first and second duet samples, we used main-effects ANOVA to compare 12 duet variables between pairs and years, or between pairs and seasons. This analysis compared the effect of factors ‘pair identity’ and ‘year’ or ‘pair identity’ and ‘season’ on each variable. Also, the main-effects ANOVA *F*-ratios revealed which variables contributed most to pair vocal identity.

For the first duet sample we also used discriminant analysis (DFA) forward stepwise procedure to determine whether duets could be assigned to the correct pairs within years. Maximum and peak fundamental frequencies were highly positively correlated with each other, so we included in DFA only 10 variables (without *Fpeak_M* and *Fpeak_F*). We used DFA Wilks’ Lambda values to estimate the contribution of each variable to classification. To identify pairs ~10 years later, we used cross-validation. We used DFA functions calculated for the samples of duets in the first time period (2003–2006) to discriminate duets in the second period

(2013–2015). We calculated the percentage of the correct classification due to chance by applying a randomization procedure. The expected level of correct assignment was averaged from DFAs performed on 1000 randomized permutations of the data set (Solow 1990).

For first and third duet samples we used Paired *t* test to compare the duet variables of each pair between years and of each bird before and after pair-mate change.

We used the Benjamini–Hochberg procedure (Benjamini and Hochberg 1995) to control the false discovery rate. The randomization test was performed using MASS package of R 2.11.1. (Team 2009). All other statistical analyses were conducted using STATISTICA v. 8.0 (StatSoft, Inc., Tulsa, OK, USA).

Results

With main-effects ANOVA, we tested the effect of ‘pair identity’ and ‘year’ or ‘pair identity’ and ‘season’ on the duet variables (Table 2). Pairs differed on all variables in both analyses, whereas years differed on 7 of 12 variables and seasons differed on 8 of 12 variables. Comparison of *F*-ratios showed that the effect of pair identity on syllable variables was always stronger than the effect of the year or season. Between-pair variability was highest in measures of fundamental frequency (Table 2).

We checked the stability of duet variables over ~ 10 years using DFA with the following cross-validation procedure. First, we independently calculated DFA functions for two data sets from the first duet sample (2003–2006 and 2013–2015). In both cases DFA performed on 10 duet variables showed 100% of correct classification to a pair

(Table 3; Online Resource 1). Since none of the 1000 values of random correct assignment obtained via randomization procedure exceeded the original percent of correct classification via DFA on both data sets (means: $46.4 \pm 4.0\%$ and $47.7 \pm 4.3\%$, respectively; $n = 1000$) we reached the conclusion that the reliability of the original classification is significantly higher than those computed by chance ($p < 0.001$). The variables that contributed most to discrimination were *Fmin_M*, *Fmin_F*, *Dur_M*, *Dur_Syll*, and *Fmax_F*. Second, we performed the cross-validation procedure: discriminant functions generated on the training set of duets (2003–2006) applied to the test set (2013–2015) showed a high percentage of correct classification to a pair as well (93%; Table 3). This value was significantly higher than the percent of correct assignment due to chance (randomization procedure: $47.1 \pm 4.1\%$; $n = 1000$; $p < 0.001$).

With Paired *t* test, we found that most variables did not differ between time periods for each of the 10 pairs (Fig. 2, Online Resource 2), whereas those variables differed significantly between pairs (Table 2). However, throughout the study period, fundamental frequency declined slightly in ten birds of 20 (5 males and 5 females); fundamental frequency increased slightly in one female, and temporal variables changed in two males and one female (Paired *t* test). Despite these small changes, the duets in general remained recognizable via the whole set of variables (Table 3). It is interesting to note that the decrease in fundamental frequency measures (which made the greatest contribution to DFA classification) were the most common changes we noted over the study. In addition, they occurred most often in the oldest birds, that were > 17 years old at the time of the first recording (in six of the nine birds of this age, Fig. 2, Online Resource 2). For birds that were < 10 years of age when first recorded,

Table 2 Main-effects ANOVA results for the effect of factors ‘pair identity’ and ‘year’ or ‘pair identity’ and ‘season’ on duet variables in the Siberian Cranes (*Leucogeranus leucogeranus*)

Duet variable	Between-year variability ($n = 219$)				Between-season variability ($n = 329$)			
	Pair effect		Year effect		Pair effect		Season effect	
	<i>F</i> _{9,208}	<i>p</i>	<i>F</i> _{1,208}	<i>p</i>	<i>F</i> _{10,316}	<i>p</i>	<i>F</i> _{2,316}	<i>p</i>
Dur_Duet	9.2	< 0.0001	3.8	0.054	16.4	< 0.0001	4.5	0.012
Dur_Syll	114.9	< 0.0001	15.2	0.0001	101.1	< 0.0001	12.0	< 0.0001
Dur_M	131.5	< 0.0001	7.0	0.009	111.2	< 0.0001	5.6	0.005
Dur_F	44.0	< 0.0001	0.8	0.366	157.7	< 0.0001	1.7	0.183
Dur_MF	6.8	< 0.0001	0.0	0.940	9.5	< 0.0001	0.2	0.786
Dur_FF	33.3	< 0.0001	3.5	0.064	58.6	< 0.0001	1.9	0.142
Fpeak_M	186.8	< 0.0001	99.4	< 0.0001	664.0	< 0.0001	5.0	0.005
Fmax_M	183.7	< 0.0001	150.6	< 0.0001	608	< 0.0001	2.0	0.216
Fmin_M	241.8	< 0.0001	75.8	< 0.0001	921.1	< 0.0001	4.9	0.006
Fpeak_F	185.9	< 0.0001	3.9	0.050	284.2	< 0.0001	42.2	< 0.0001
Fmax_F	161.5	< 0.0001	22.2	< 0.0001	363.0	< 0.0001	31.0	< 0.0001
Fmin_F	155.8	< 0.0001	32.5	< 0.0001	374.0	< 0.0001	60.0	< 0.0001

Bold text indicates a significant fit according to Benjamini–Hochberg procedure

Table 3 Percentages of duets correctly classified to pairs with discriminant function (DFA) and cross-validation analyses for 10 Siberian Crane (*Leucogeranus leucogeranus*) pairs; *n*—the number of duets, included into analysis, %—the percentage of correctly assigned duets, recording periods are given in brackets

Pair	Discrimination		Cross-validation		Discrimination	
	<i>n</i> (2003–2006)	%	<i>n</i> (2013–2015)	%	<i>n</i> (2013–2015)	%
1	12	100	12	100	12	100
2	12	100	12	100	12	100
3	12	100	12	91	12	100
4	7	100	12	75	12	100
5	12	100	12	100	12	100
6	12	100	12	100	12	100
7	10	100	12	66.7	12	100
9	9	100	9	100	9	100
10	12	100	4	100	4	100
12	12	100	12	100	12	100
Total	110	100	109	92.7	109	100

we found no changes in the fundamental frequency (Fig. 2, Online Resource 2).

Finally, we found little change in acoustic variables after a re-mate (Online Resource 3). For instance, no changes in variables occurred in calls of male #10, but the total duet duration increased significantly after he re-mate. Calls of female #8 increased slightly in duration, and duration and fundamental frequency of calls of female #11 decreased (Paired *t* test, Online Resource 3). However, these changes did not exceed those noted in birds living with one partner throughout the study (Online Resource 2). A decrease in fundamental frequency also occurred in the oldest bird (female #11, she was 27 years old before she changed her mate), while male #10 (12 years old) and female #8 (14 years old) did not change the fundamental frequency of their calls (Online Resource 3).

Discussion

Long-term stability of Siberian Crane duets and perspectives of the vocal-based monitoring

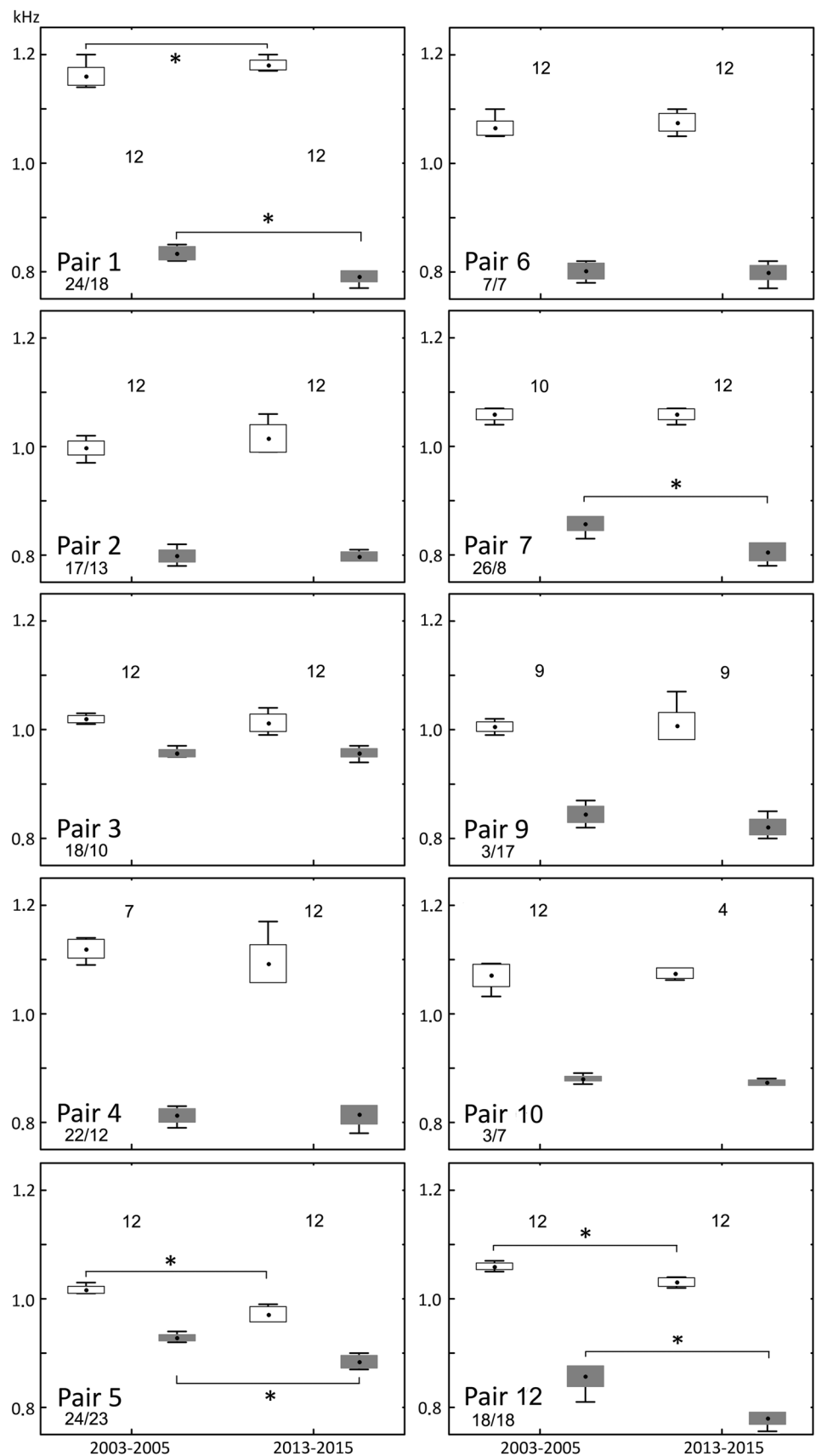
We showed that Siberian Crane pairs can be identified very accurately based on temporal and frequency attributes of their duets. This held over different seasons within years, and across ~10 years. The effect of pair identity on acoustic variables was much stronger than the effect of the year or season.

To our knowledge, the period of vocal stability that we observed far exceeds that known for other birds. The use of data from captive birds allowed us to be confident in the identity of examined birds throughout all the 15 study years. At the same time, the majority of studies focused on retained identity in bird calls use mostly the data obtained on the unmarked wild individuals, basing on similarity in call structures, recorded repeatedly at the same home territory (e.g. Gilbert et al. 1994, 2002; Galeotti and

Sacchi 2001; Delport et al. 2002; Tripp and Otter 2006; Grava et al. 2008; Policht and Tichackova 2010; Odom et al. 2013). However, the scarce data from marked birds showed that in some species individuals had changed their calls with time (Eakle et al. 1989; Guyomarc'h et al. 1998; Puglisi and Adamo 2004; Walcott et al. 2006; Volodin et al. 2008; Cornec et al. 2015; Humphries et al. 2016). In mammals, a lack of temporal stability of individually specific call variables appears to be even more common than in birds (Jorgensen and French 1998; Snowdon and Elowson 1999; Rukstalis et al. 2003; Chulкина et al. 2006; Matrosova et al. 2009, 2010); however, cases of more than 20-year retention of individually specific vocal signatures are also known (e.g. Luís et al. 2016). On the other hand, most studies that considered the stability of individual features, traced it only for 1–2 years (Jones et al. 1993; Lengagne 2001; Laiolo et al. 2007; Klenova et al. 2012; Petruskova et al. 2016; Gonzalez-Garcia et al. 2017; Dent and Molles 2016), rarely for 3–5 years (Klenova et al. 2009; Kirschel et al. 2011). Our research is one among the few that confirmed the stability of vocal individuality in a bird species (namely, the Siberian Crane) for such a long time (~10 years).

Long-term stability in the crane vocal duets suggests that it may be useful for individual recognition not only during a single breeding season, but also on the wintering grounds or on the breeding grounds over years (and possibly the whole lifetime). Long-term vocal stability may also provide Siberian Cranes the opportunity to form long-term social bonds with neighbours on the nesting grounds, which could minimize the energy expended on aggressive behaviour and reduce escalated conflicts between neighbours ('dear enemy phenomenon', Fisher 1954; Briefer et al. 2008). Such economy could be especially useful at the beginning of each breeding season, especially for a species that breeds in a polar regions where dates of arrival at the nest territories and egg laying are pronouncedly determined by year-to-year

Fig. 2 Changes that occurred in ~ 10 years in two duet variables in 10 examined Siberian Crane (*Leucogeranus leucogeranus*) pairs. Fpeak_M—grey boxes, Fpeak_F—white boxes, points represent means, boxes—SD, whiskers—Min–Max, *—significant difference according to Benjamini–Hochberg procedure, Paired *t* test. Numbers above the boxes show the *n* of analysed duets for each pair for each year. In the lower left corner of each graph, the ages of the male/female of the pair at the moment of first recording are given



variation in weather and seasonality (e.g. Archibald and Lewis 1996).

The present study encourages the use of the vocal-based monitoring for censuses and conservation of Siberian Crane. In case of cranes acoustic monitoring is preferred over to leg, neck and radio tagging as a non-invasive tool, since cranes are extremely difficult to catch, and the existing methods of catching are highly traumatic. Also, neck collars and other tags may reduce survival rate and change the behaviour of birds (Menu et al. 2000; Schmutz and Morse 2000; Irvine et al. 2007; Fremgen et al. 2017). More than that, for birds living in dense grass (e.g. corncrakes, bitterns and cranes), and for nocturnal species as owls, acoustic monitoring is often the only appropriate method. At the same time, modern technologies, such as automated field recorders and sound recognition software, make vocal monitoring an increasingly more affordable and efficient method (Mennill et al. 2006; Blumstein et al. 2011; Frommolt and Tauchert 2014). As a non-invasive tool for the breeding pairs identification, the vocal-based monitoring may also help to extend knowledge on biology of the poorly studied species. For instance, it could provide information about home ranges, territory fidelity and population numbers in different localities. Our results suggest that Siberian Crane duets can potentially be used for breeding pairs' identification in the wild, and together with data obtained on other crane species (Klenova et al. 2009; Policht and Tichackova 2010), we can conclude that stability of individually specific features in duets through years are typical for cranes in general, so that the perspectives of the vocal-based monitoring for the entire group are promising.

Effect of pair-mate change on acoustic variables of Siberian Crane duets

In our study we also analysed for the first time the influence of the pair-mate change on the stability of the duet variables of individual cranes. Since both stability (e.g. Jones et al. 1993; Lengagne 2001; Laiolo et al. 2007; Klenova et al. 2009, 2012; Kirschel et al. 2011; Petruskova et al. 2016; Gonzalez-Garcia et al. 2017) and instability patterns (e.g. Eakle et al. 1989; Guyomarc'h et al. 1998; Puglisi and Adamo 2004; Walcott et al. 2006; Cornec et al. 2015; Humphries et al. 2016) have been reported previously for individually specific vocal features, it would be interesting to understand which factors can affect it. The vocal patterns could be affected by social and environmental contexts both in songbirds (e.g. Nowicki 1989; Hile et al. 2000) as well as in species without vocal learning (mammals: Snowdon and Elowson 1999; Rukstalis et al. 2003; birds: Walcott et al. 2006). We found almost no effect of re-mate on the stability of the duet variables in Siberian Cranes. So, Siberian Cranes possibly do not perfectly adjust their vocal characteristics

to the vocal characteristics of a new mate, but our data do not prove the absolute absence of socially determined vocal plasticity in Siberian Cranes. A lot of other factors, such as population density or presence of a rival, could cause vocal tuning in species both with and without vocal learning (e.g. Howard and Young 1998; Penteriani 2003; Brumm 2009). The impact of social factors on acoustic variables of Siberian Crane duets is still unknown. Also, our conclusion is limited, since it is based on a sample of only three birds. Indeed, the pair-breaks in cranes occur quite rare both in nature (Littlefield 1981; Nesbitt 1989; Hayes 2005; Henne and Blahy-Henne 2013) and in captivity (pers. obs.), and these three cases of re-mates are all that we were able to collect in 15 years of study. Therefore, additional researches are still required to prove or disprove the absence of re-mate effect on the stability of the duet variables in Siberian Cranes.

Fundamental frequency decrease in older Siberian Cranes

Apart of general long-term stability of Siberian Crane duets, we also found slight decrease in fundamental frequency in 10 birds out of 20. These changes occurred most often in oldest birds that were first recorded at 18 years old or more (Fig. 2, Online Resource 2). The young birds (that were first recorded at < 10 years old), did not show any changes in the fundamental frequency (Fig. 2, Online Resource 2). These findings may indicate the presence of some keys to the individual age in Siberian Crane duets. It can be an important information, since accumulating evidence suggests that age is related to the quality of individuals (e.g. Manning 1985). Indeed, it is believed that the older birds have proved their higher quality through their longevity and have acquired more experience in foraging or in behaviours related to reproductive success (Martin 1995). The playback studies showed that several bird species can recognize the songs of young and old males (Cucco and Malacarne 1999; Balentine 2009; de Kort et al. 2009 etc.). Information about age can be encoded in various acoustic variables, ranging from subtle changes in temporal or spectral characteristics to structural patterns such as the size or composition of repertoires and the delivery of repertoires (Kipper and Kiefer 2010). For songbirds the most commonly seen scenarios include an increase of song consistency and/or song complexity to maturation and their fall with senescence (Kipper and Kiefer 2010; Rivera-Gutierrez et al. 2012; Zippel et al. 2019 etc.). However, fundamental frequency of calls has been rarely tested for age variability in birds. Few studies have shown that it can change with age differently in different passerine species (Bjorklund 1989; Cucco and Malacarne 1999; Garamszegi et al. 2005), but in mammals it usually decreases (Reby and McComb 2003; Fischer et al. 2004; Charlton et al. 2009; Mathevon et al. 2010 etc.).

Unfortunately, for non-passerines the studies of age-related changes in vocal behaviour are currently absent. Further investigations of fundamental frequency variability with age in this group of species may shed light on the existence of certain fundamental principles for encoding information on age in the sounds of mammals and birds that do not possess vocal learning.

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Compliance with ethical standards

Conflict of interest Authors have no conflict of interest to declare.

Ethical approval Data collection protocol #2003–2014 was approved by the Committee of Bioethics of Lomonosov Moscow State University.

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