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MODELLING BIOACOUSTICAL MONITORING THROUGH YEARS WITH CAPTIVE POPULATION OF THE RED-BREASTED GOOSE

I. A. Volodin[1,2], A. V. Klenova[1], E. V. Volodina[2]

[1] Moscow State University, Moscow, Russia; *volodinsvoc@mail.ru*
[2] Moscow Zoo, Moscow, Russia

INTRODUCTION

In the last decades, bioacoustical methods were developing quickly and showed their applicability to solvation of both fundamental and practical tasks. The call-based methods for species recognition and censuses have proved their efficiency for many passerine and non-passerine bird species (*see* review by Baptista, Gaunt, 1997).

Recently, along with monitoring and censuses of species, it became possibly to conduct bioacoustical monitoring of individuals, i.e., to track particular birds by their calls. Developing a method for individual call-based monitoring is especially important for rare bird species. For the bird tracking by their voices, it is necessary, at first, to reveal individual features in calls, and, second, to investigate stability of these features from year to year (Володин и др., 2005).

In the case when individual characteristics are well expressed in calls and remain intact throughout the life of a bird, we receive a possibility to distinguish a certain individual reliably among others without capture, marking or other traumatic procedures. Thus, sometimes the bioacoustical monitoring may be good alternative to common methods of bird tracking (for example, ringing) and could be useful for thorough studying the details of biology of some poorly investigated species (Volodina et al., 2004).

It should be noticed that the individuality in call features was found in a lot of bird species lacking external sexual dimorphism (e.g., Falls, 1982; Hausberger et al., 1991; Guyomarc'h et al., 1998; May, 1998; Aubin, Jouventin, 2002; Volodina, Volodin, 2003). However, sustainability of individual characteristics in bird and mammalian calls from year to year was examined only in a few studies, results of which are contradictory as a rule (Jorgensen, French, 1998; Reby et al., 1998; Delport et al., 2002;

Володин, Матросова, 2004; Chulkina et al., 2006). Meanwhile, chances to record a few calls from a given individual and to use them throughout the following years for tracing its movements, nesting conservatism or breeding success seem very attractive.

In addition to monitoring individual birds, the second important direction of bioacoustical research is focused on sexual differences in calls of bird species lacking external sexual dimorphism. Information concerning sexual differences in calls may be useful both for noninvasive bioacoustical sexing of captive birds and for receiving information about sex ratios in censuses of wild populations (Carlson, Trost, 1992; Nuechterlein, Buitron, 1992; Smith, Jones, 1997; Klenova et al., 2004; Volodin et al., 2003; 2005a; 2005b).

The object animal of this study was the red-breasted goose (*Branta ruficollis*). The red-breasted goose is the species lacking apparent sexual dimorphism both in size and coloration. During the nesting period, the birds could be relatively easily sexed according to their behaviour, while in non-breeding period sexing appears to be almost impossible without capture (Volodin, 1990a; 1990b). The problem of noninvasive monitoring is topical for this species, because this is the rare species with its breeding grounds restricted to Russia. In the 1980s, population number of this species in nature decreased abruptly from 75 000 to 30 000 birds (Кривенко и др., 1983); however, by the late 1990s the number of the red-breasted geese has increased up to 80 000 and continues to grow (Syroechkovski Jr., 1995; 1999; Dereliev, 1998; Kharitonov, 2005).

The red-breasted goose is also an appropriate species for bioacoustical monitoring, because this method is assumed to be especially effective for the species nesting in small colonies with easily detected individual territories and producing loud sounds. The red-breasted geese nest in small colonies of up to eight pairs, the neighboring colonies often situated up to 10 km apart, on the hills along shorelines of the tundra rivers near the nests of the peregrine falcons (*Falco peregrinus*) and snowy owls (*Nyctea scandiaca*) (Наумов, 1931; Quinn et al., 2003; Kharitonov et al., 2005). The birds of both sexes, especially males, often produce loud two-syllable calls, using them for mobbing Arctic foxes, dogs and humans (S.P. Kharitonov, J.I. Kokorev, J.L. Quinn, pers. comm.). The red-breasted geese also often produce loud two-syllable calls in captivity, especially in spring, during the breeding season (Volodin, 1990c).

Therefore, these calls of red-breasted geese could be easily recorded in the wild without disturbance of birds, and small colony sizes allow reliable distinguishing of the caller's personality. For the red-breasted goose, bioacoustical monitoring can answer the following questions: whether pairs return to their former nests, whether pairs bonds are maintained for years, and whether young birds return to their "parental" colonies or disperse to the new nesting grounds.

However, the only way to develop a method for individual identification is gathering records from the same individuals from year to year. As a rule, it is possible only with birds kept in captivity or in semi-captive conditions. This was the reason why our research was carried out on the group of red-breasted geese kept for a few years in the Moscow Zoo.

The goals of our study were to compare the degrees of individual and sexual differences in the loud two-syllable calls; examine the reliability of individual identification of red-breasted geese throughout a few years; and estimate possibility of bioacoustical monitoring for this species in the wild.

MATERIAL AND METHODS

In the study we used calls from 36 adult red-breasted geese (22 males and 14 females) recorded in Moscow Zoo throughout five breeding seasons, from 1985 to 1989. Most of the birds (17 males and 13 females) were captured on Taimyr Peninsula, the rest 5 males and a female were descendents of captive breeders. The geese were kept in separate groups of 4 to 17 individuals (for details see: Володин, 1991a; Volodin, 1992). All birds were individually marked with the sets of colour leg rings. Birds were sexed by cloak inspection and in some cases sexing was confirmed post mortem.

For audio recording we used a Reporter-5P tape-recorder with MKE-2 condensed unidirectional microphone. This acoustic system provided high-quality recordings from 50 Hz to 12 kHz. Loud, distant, two-syllable calls of the red-breasted geese were recorded throughout a year, but mainly in spring, before and during the breeding season. Spontaneous calls were recorded during territorial displays. Calls of one pair often stimulated vocalization of the neighboring pairs (Volodin, 1990c; Володин, 1991b). Some calls were also recorded in the pair mates separated during handling procedures (weighting, examinations, etc.). The males produced sounds in both situations, whereas the females called mainly in the latter. All the recordings were made outdoors. The orientation of a bird to the microphone varied both within and between the recordings; the distance to a bird varied from 2 to 10 m.

Both digitizing (sampling frequency 22.05 kHz) and sound analyses were made with Avisoft-SASLab Pro v. 4.2. (© R. Specht). Spectrograms were computed with Hamming Window, a FFT length of 512 points, a frame of 50 %, and an overlap of 93.75 %. These settings provided a bandwidth of 112 Hz, a frequency resolution of 43 Hz and a time resolution of 1.5 ms. In total, we analysed 1328 calls, from 2 to 141 per individual.

For the spectrogram analysis, after high-pass filtration at 500 Hz for background noise removing, we used the "automatic parameter measurements" option for power parameter set extraction. Both in the single and mean power spectra (in our case, the single time window is equal to 1.5 ms), this option allowed us to measure the frequency of maximum amplitude, bandwidth on the level of -10 dB below the maximum amplitude and three quartiles of a spectrum, the lower, middle and upper ones (the frequencies delimiting from above 25, 50 and 75 % of the total power energy, respectively) (Fig. 1). In addition, for each power spectrum, the entropy, allowing the quantitative estimation of noisy and harmonic energy in a power spectrum, was measured. The entropy was automatically calculated as a ratio of geometrical-to-arithmetical mean; its value varied from 0 (for a pure tone) to 1 (for a white noise).

For each two-syllable call, 55 parameters were measured: intersyllable interval and 27 parameters for each of two syllables:

1) Two temporal parameters: overall duration and duration from the beginning of a syllable to the point of maximum amplitude;

2) Seven parameters of mean power spectrum of a syllable: frequency of maximum amplitude, bandwidth, three quartiles, entropy, and the dominant frequency range;

3) Two parameters for each of 9 single power spectra, taken automatically with equal intervals from the beginning to the end of a syllable (Fig. 1): frequency of maximum amplitude and middle quartile.

We did not measure fundamental frequency values, because in many two-syllable calls the fundamental frequency was masked by numerous nonlinear phenomena, mainly by deterministic chaos and sidebands (*see* Fee et al., 1998; Larsen, Goller, 1999; Lavenex, 1999). Therefore, we took for estimation of structural variability only temporal and power parameters, measurable in calls of any structure. As a rule, birds produced bouts of up to a few dozens of two-syllable calls. However, intercall intervals between the two-syllable calls were not measured, because a few birds often called simultaneously. Thus, during recording sessions we commented identity only for separate calls, not for entire bouts.

For statistical analyses, we used methods of multivariate statistics (one-way ANOVA, discriminant and cross-validation analyses). As long as the results of discriminant analysis are strongly dependent on the differences in group samples (Titus et al., 1984), for analysis of individual and sexual differences we formed equal samples for each group with random selection of values from the entire data pool.

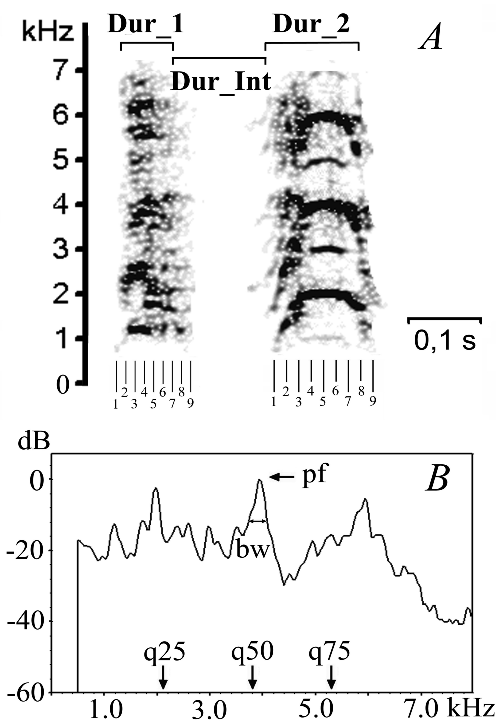

Fig. 1. Parameter measurements taken from the two-syllable call of the red-breasted goose.
A (spectrogram): **Dur_1 –** duration of the 1st call syllable; **Dur_2 –** duration of the 2nd call syllable; (**Dur_Int**) – intersyllable interval; **1–9** – measurement points of the single power spectrum parameters;
B (mean power spectrum): **pf –** frequency of maximum amplitude; **bw –** bandwidth –10 dB from maximum amplitude; **q25 –** lower quartile of the spectrum; **q50 –** middle quartile; **q75** – upper quartile.

Рис. 1. Измеряемые параметры в двухударном крике краснозобой казарки.
А (спектрограмма): **Dur_1 –** длительность первого слога крика; **Dur_2 –** длительность второго слога крика; **Dur_Int –** длительность интервала между первым и вторым слогами; **1–9** – места измерений параметров точечных энергетических спектров;
В (энергетический спектр): **pf –** доминантная частота; **bw –** ширина частотного пика на уровне –10 дБ от максимальной амплитуды; **q25** – нижняя квартиль спектра; **q50 –** средняя квартиль; **q75** – верхняя квартиль.

We included into analysis on individual variability the calls recorded from 22 birds (17 males and 5 females), 16 to 20 calls per bird, and 430 calls in total. In cases when the number of calls from a bird exceeded 20, selection was made accordingly to the principle of maximum diversity. For example, if calls of a given bird were recorded in more than one breeding season, we included into a sample the equal number of calls from each year (i.e., if the calls were recorded during two years, the sample was comprised of 10 calls recorded in the first year and 10 calls recorded in the second year).

We included into analysis on sexual variability the calls recorded from 22 males (three calls per male) and from 12 females (4–5 calls per female), 125 calls in total. For this analysis also, calls were selected accordingly to the principle of maximum diversity (for example, in the case when calls of a given male were recorded throughout three years, we included 1 call per year into the sample).

For analysis of stability in calls through years, we used only male spring calls, and only from males with no less than 4 recorded calls per spring. To find the better way of individual identification in the following years, we applied two approaches of preparing samples for cross-validation procedures. With the first approach (successive), we counted discriminate functions for calls recorded during a given year, and then used these functions for discrimination of calls recorded in the following year. With the second approach (cumulative), we counted discriminate functions for pooled samples for calls recorded during a few sequential years, and used them for discrimination of calls recorded during the following year.

To calculate random values for correct assignment percentages of discriminant analysis, we applied randomization procedure (Solow, 1990) that allows considering that some parameters may not be entirely independent. To run the randomization procedure, we created randomization groups, equal to the number of groups included into discriminant analyses and consisting of the equal number of calls randomly selected from each individual (for the analysis on assignment to individual) or for each sex (for the analysis on assignment to sex). After that, we conducted discriminant analysis forward stepwise procedures for probability of correct assignment of calls to randomization groups and took their results as random values for assignment to individual and to sex, respectively. Differences between the random and actual values of the correct assignment were tested with 2x2 χ^2 test.

All statistical analyses were made in STATISTICA, v. 6.0 (StatSoft, Inc).

RESULTS

Individual differences in two-syllable calls

We included into analysis on individual variability calls recorded from 22 birds (16 to 20 calls per bird, 430 in total). ANOVA showed highly significant individual differences for all 55 parameters of the two-syllable calls. The greatest individual differences were found in the following parameters: intersyllable interval ($F_{21.408}$ = 75.07); duration of the second syllable ($F_{21.408}$ = 41.14), and duration of the period from the beginning of the second syllable to the point of maximum amplitude ($F_{21.408}$ = 25.58); all differences were significant ($p < 0.001$). Average values of some parameters of the two-syllable calls of 22 individual red-breasted geese are given in Table 1.

Table 1
Values (mean ± SD) of the two-syllable call power and temporal parameters for 22 red-breasted geese and results of ANOVA analysis for individual differences
Таблица 1
Значения (среднее ± SD) параметров двухударных криков 22 краснозобых казарок и результаты межиндивидуального сравнения при помощи однофакторного дисперсионного анализа (ANOVA)

Individual / Особь	N	Dur_Int, ms	Dur_1, ms	Dur_2, ms	pf_mean1, kHz	pf_mean2, kHz
Male 1 / Самец 1	20	219±18	75±8	105±11	2.78±1.43	2.63±1.08
Male 4 / Самец 4	20	106±49	82±11	195±40	2.47±0.96	3.14±1.02
Male 5 / Самец 5	20	212±26	77±7	104±10	2.57±1.06	2.52±0.76
Male 7 / Самец 7	20	168±34	82±7	108±17	2.53±0.75	2.54±0.96
Male 8 / Самец 8	20	118±25	82±7	85±13	2.10±0.32	2.17±0.54
Male 9 / Самец 9	20	138±25	83±6	104±10	2.96±1.17	2.98±1.32
Male 10 / Самец 10	20	295±42	79±10	93±12	3.38±1.25	3.08±1.27
Male 12 / Самец 12	20	169±15	71±8	91±7	1.99±0.79	2.02±0.98
Male 15 / Самец 15	20	325±31	83±9	140±30	2.17±0.17	2.31±1.21
Female 19 / Самка 19	18	124±55	90±8	113±35	2.00±0.52	2.02±0.46
Female 23 / Самка 23	20	135±16	98±7	156±16	1.65±0.26	1.78±0.72
Female 28 / Самка 28	20	152±28	78±10	97±9	2.52±1.20	1.90±0.81
Male 31 / Самец 31	16	288±55	89±5	133±13	2.23±0.23	2.12±0.19
Male 41 / Самец 41	20	235±54	82±7	111±19	3.40±1.31	2.94±1.07
Male 44 / Самец 44	20	165±24	92±13	120±21	2.75±1.03	2.95±1.55
Male 48 / Самец 48	20	182±33	90±5	168±14	2.20±0.56	1.89±0.09
Male 49 / Самец 49	20	172±18	86±7	114±12	2.15±0.63	1.89±0.24
Male 101 / Самец 101	20	260±42	84±6	132±22	4.05±1.24	2.27±0.85
Female 107 / Самка 107	20	88±15	79±11	101±21	1.97±0.30	2.45±0.30
Female 110 / Самка 110	16	179±40	93±12	137±17	2.00±0.21	2.15±0.55
Female 113 / Самка 113	20	86±19	80±5	148±19	2.17±0.25	1.97±0.40
Male 118 / Самец 118	20	169±31	89±5	104±14	2.15±0.53	2.86±1.38
ANOVA		F = 75.07 p < 0.001	F = 12.28 p < 0.001	F = 41.14 p < 0.001	F = 8.90 p < 0.001	F = 4.63 p < 0.001

Notes: *N* – number of calls; Dur_Int – intersyllable interval; Dur_1 and Dur_2 – durations of the 1st and 2nd syllables; pf_mean1 and pf_mean2 – frequencies of the maximum amplitude of the 1st and 2nd call syllables.

Прим.: *N* – число криков; Dur_Int – длительность интервала между слогами; Dur_1 и Dur_2 – длительности первого и второго слогов; pf_mean1 и pf_mean2 – частоты максимальной амплитуды первого и второго слогов.

Discriminant stepwise analysis based on 50 of 55 call parameters showed 85.6 % correct assignment to individual, which was significantly higher than the random value (14.7 %) calculated with randomization procedure ($\chi^2 = 429.8$, $df = 1$, $p < 0.001$). Individual scores of discrimination varied from 66.7 to 100 % (Table 2). Four parameters, in order of decreasing importance, have mainly contributed into discrimination: the intersyllable interval, duration of the second syllable, the lower quartile

Table 2
Assignment of red-breasted goose calls to a correct caller on the basis of stepwise discriminant and cross-validation analyses
Таблица 2
Причисление криков краснозобых казарок к данной особи на основе пошагового дискриминантного и кроссвалидационного анализов

Individual Особь	Discriminant analysis Дискриминантный анализ		Cross-validation analysis Кроссвалидационный анализ	
	N	Correctly classified Правильно причислено (%)	*N*	Correctly classified Правильно причислено (%)
Male 1 / Самец 1	20	80	121	39.7
Male 4 / Самец 4	20	95	52	50
Male 5 / Самец 5	20	70	111	39.6
Male 7 / Самец 7	20	80	49	30.6
Male 8 / Самец 8	20	100	56	71.4
Male 9 / Самец 9	20	90	58	36.2
Male 10 / Самец 10	20	75	97	62.9
Male 12 / Самец 12	20	85	14	57.1
Male 15 / Самец 15	20	95	6	66.7
Female 19 / Самка 19	18	66.7	0	0
Female 23 / Самка 23	20	90	54	87
Female 28 / Самка 28	20	90	64	29.7
Male 31 / Самец 31	16	93.8	0	0
Male 41 / Самец 41	20	65	83	33.7
Male 44 / Самец 44	20	75	1	0
Male 48 / Самец 48	20	95	1	100
Male 49 / Самец 49	20	80	8	37.5
Male 101 / Самец 101	20	85	7	28.6
Female 107 / Самка 107	20	95	26	76.9
Female 110 / Самка 110	16	87.5	0	0
Female 113 / Самка 113	20	100	9	66.7
Male 118 / Самец 118	20	90	3	66.7
Total / Всего	**430**	**85.6**	**820**	**48.2**

Notes: *N* – number of calls.
Прим.: *N* – число криков.

of mean power spectrum of the first syllable, and duration of the first syllable. Figure 2 illustrates individual differences in the structure of two-syllable calls of six male red-breasted geese.

To validate results of discriminant analysis, we conducted cross-validation analysis. With cross-validation analysis, discriminant keys derived from one sample (training data set) are used for classification of another sample (testing data set). We used as a testing set the rest 820 two-syllable calls recorded from 22 individuals, subjected to analysis on individual call differences (Table 2). The cross-validation analysis showed the lower correct assignment of 48.2 %, which nevertheless exceeded significantly the random value ($\chi^2 = 135.1$, $df = 1$, $p < 0.001$).

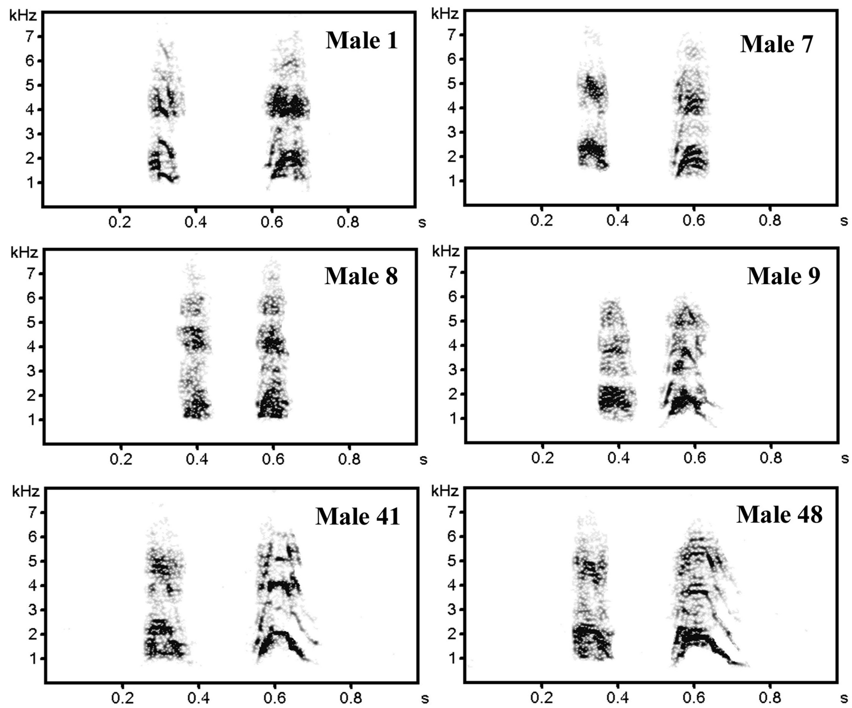

Fig. 2. Individual differences in two-syllable calls of six male red-breasted geese (one call per male). Note the differences in intersyllable intervals and durations of the 1st and 2nd syllables.

Рис. 2. Индивидуальные различия в двухударных криках шести самцов краснозобых казарок (по одному от каждого). Обратите внимание на различия в межслоговом интервале и длительностях первого и второго слогов.

Similar discriminant stepwise analyses on assignment to individual were performed for each sex separately. For 17 males ($n = 336$ calls), the average correct assignment percentage was 89.0 % with random 30.1 % (differences were significant, $\chi^2 = 239.7$, $df = 1$, $p < 0.001$); cross-validation with the rest 731 calls showed average correct assignment of 51.2 %. For 5 females ($n = 94$ calls), discriminant analysis showed 98.9 % correct assignment, with random value of 56.4 % (differences were significant, $\chi^2 = 46.6$, $df = 1$, $p < 0.001$); cross-validation with the rest 89 calls showed 65.2 % correct assignment. The same parameter (intersyllable interval) had mainly contributed into discrimination both in males and in females; duration of the second syllable was the second in its contribution to discrimination for males and the third for females.

Sexual differences in two-syllable calls

We included into analysis on sexual variability calls from 22 males (3 calls per male) and from 12 females (4–5 calls per female), 125 calls in total. ANOVA showed significant differences between sexes only for 45 of 55 parameters. The greatest differences between sexes were found in the following parameters: upper quartile of mean power spectrum of the first syllable ($F_{1.123} = 56.32$); upper quartile of mean power spectrum of the second syllable ($F_{1.123} = 55.98$), and middle quartile of the third single power spectrum of the first syllable ($F_{1.123} = 49.51$); all differences were significant ($p < 0.001$). Average values for five parameters of two-syllable calls for male and female red-breasted geese are given in Table 3.

However, discriminant stepwise analysis based on 19 of 55 call parameters has revealed virtually no sexual differences in two-syllable calls of the red-breasted geese. Although the correct assignment to sex was 87.2 % (Table 4), this value did not differ significantly from random value (79.2 %) calculated with randomization procedure ($\chi^2 = 2.32$, $df = 1$, $p = 0.128$). Four parameters, in order of decreasing importance, have mainly contributed into discrimination: upper quartile of mean power spectrum of the first syllable; middle quartile of sixth single power spectrum of the second syllable, bandwidth of mean power spectrum of the second syllable, and entropy of mean power spectrum of the first syllable. Cross-validation analysis conducted with the rest 1203 calls also showed 81.7 % correct assignment. This value did not differ significantly from the random value of assignment to sex ($\chi^2 = 0.33$, $df = 1$, $p = 0.568$).

Call stability through years

We used two approaches for analysis of call stability through years in male red-breasted geese. With the first approach (successive), we calculat-

Table 3
Values (mean ± SD) of the two-syllable call power and temporal parameters for male and female red-breasted geese and results of ANOVA analysis for sexual differences
Таблица 3
Значения (среднее ± SD) параметров двухударных криков самцов и самок краснозобых казарок и результаты межполового сравнения при помощи однофакторного дисперсионного анализа (ANOVA)

Sex / Пол	N	Dur_Int, ms	Dur_1, ms	Dur_2, ms	pf_mean1, kHz	pf_mean2, kHz
Males / Самцы	66	193±71	80±11	115±26	2.73±1.05	2.50±0.98
Females / Самки	59	151±81	85±12	117±31	2.15±0.54	2.15±0.61
ANOVA		F = 9.61 $p < 0.05$	F = 7.05 $p < 0.05$	F = 0.13 ns	F = 14.72 $p < 0.001$	F = 5.41 $p < 0.05$

Notes: ns – differences are non-significant; other abbreviations as in Table 1.
Прим.: ns – различия недостоверны; остальные обозначения как в таблице 1.

ed discriminate functions for calls recorded during a given year, and then used these functions for discrimination of calls recorded from the same individuals in the next year (Table 5). Discriminant stepwise analysis on assignment to individual performed for each of four years (within-year classification) showed very high correct assignment scores ranging from 85.8 % (1988 within-year classification for 12 males) to 100 % (1989 within-year classification for 7 males) (Table 5). In all four within-year analyses, inter-syllable interval and duration of the second syllable were those parameters that mainly contributed into discrimination. A cross-validation analysis of the calls recorded from the same birds in the next year was performed using discriminant cues calculated for the call samples of the previous years

Table 4
Assignment of red-breasted goose calls to correct sex on the basis of stepwise discriminant and cross-validation analyses
Таблица 4
Причисление криков краснозобых казарок к данному полу на основе пошагового дискриминантного и кроссвалидационного анализов

Sex / Пол	Discriminant analysis Дискриминантный анализ		Cross-validation analysis Кроссвалидационный анализ	
	N	Correct classification (%) Правильно причислено, %	N	Correct classification (%) Правильно причислено, %
Males / Самцы	66	84.8	1029	80.7
Females / Самки	59	89.8	175	88
Total / Всего	125	87.2	1204	81.7

Table 5

Assignment of male red-breasted goose calls to individual within years on the base of stepwise discriminant analysis (within-year classification) and correct assignment values of subsequent-year calls on the basis of cross-validation procedure, successive approach (between-year classification)

Таблица 5

Причисление криков самцов краснозобых казарок за текущий год к данной особи на основе пошагового дискриминантного анализа и величины правильного причисления криков следующего года на основе кроссвалидационной процедуры (последовательный подход)

Male Самец	1986 within-year classification за текущий год		1987–1986 between-year classification на следующий год		1987 within-year classification за текущий год		1988–1987 between-year classification на следующий год		1988 within-year classification за текущий год		1989–1988 between-year classification на следующий год		1989 within-year classification за текущий год	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
1	22	100	43	46.5	43	97.7	41	65.9	41	87.8	23	60.9	23	100
4	26	100	41	100	41	100								
5	43	97.7	32	68.8	32	100	45	80	45	91.1				
7	7	85.7	6	0	6	100	36	27.8	36	80.6	11	9.1	11	100
8	38	100							22	95.5	16	68.8	16	100
9									25	88	16	25	16	100
10									57	89.5				
28					40	100								
31									13	100				
41					27	96.3	42	14.3	42	64.3	28	35.7	28	100
44									13	76.9	8	12.5	8	100
49									28	89.3				
50									5	100	4	0	4	100
114									5	100				
Total Всего	136	98.5	122	68.0	189	98.9	164	48.2	332	85.8	106	38.7	106	100

Notes: *N* – number of calls; % – percentage of correctly assigned calls.
Примечания: *N* – число криков; % – доля криков, правильно причисленных данной особи.

Table 6

Assignment of male red-breasted geese calls to individual for pooled sample for a few successive years on the basis of stepwise discriminant analysis (pooled-year classification) and correct assignment values of next-year calls on the basis of cross-validation procedure, cumulative approach (between-pooled-year classification)

Таблица 6

Причисление криков самцов краснозобых казарок к данной особи на основе пошагового дискриминантного анализа за несколько предшествующих годов и величины правильного причисления криков следующего года на основе кроссвалидационной процедуры (накопительный подход)

Male Самец	1985+86 pooled-year classification суммарно по годам		1987–1985+86 between-pooled-year classification на следующий год		1985+86+87 pooled-year classification суммарно по годам		1988–1985+86+87 between-pooled-year classification на следующий год		1985+86+87+88 pooled-year classification суммарно по годам		1989–1985+86+87+88 between-pooled-year classification на следующий год		1985+86+87+88+89 pooled-year classification суммарно по годам	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
1	31	96.8	43	53.5	74	89.2	41	73.2	115	84.3	23	78.3	138	84.1
4	26	100	41	97.6	67	100			67	98.5			67	98.5
5	43	97.7	32	53.1	75	96	45	82.2	120	83.3			120	78.3
7	7	85.7	6	0	13	100	36	36.1	49	63.3	11	9.1	60	51.7
8	38	100			38	100	22	81.8	60	96.7	16	100	76	97.4
9									25	68	16	12.5	41	75.6
10									57	80.7			57	78.9
28	25	100	40	0	65	98.5			65	93.8			65	89.2
31									13	100			13	100
41					27	85.2	42	16.7	69	56.5	28	64.3	97	64.9
44									13	84.6	8	12.5	21	85.7
49									28	75			28	71.4
50									5	100	4	0	9	44.4
114									5	100			5	100
Total Всего	170	98.2	162	49.3	359	95.5	186	56.5	691	82.5	106	52.8	797	80.1

Notes: *N* — number of calls; % — the share of correctly assigned calls.

Примечания: *N* — число криков; % — доля криков, правильно причисленных данной особи.

(1987 using cues of 1986, 1988 using cues of 1987, etc.). The analysis showed remarkable decrease of assignment scores. For example, 1986 within-year classification showed average 98.5 % correct assignment to caller in comparison to 68.0 % for 1987–1986 between-year classification (Table 5).

With the second approach (cumulative), we calculated discriminant functions for pooled samples of calls recorded during a few successive years, and used them for discrimination of calls recorded from the same bird during the following year (Table 6). For pooled call samples, discriminant stepwise analysis on assignment of calls to caller also showed very high values of correct assignment, varying from 82.5 % (1985 + 1986 + 1987 + 1988 pooled-year classification for 14 males) to 98.2 % (1985 + 1986 pooled-year classification for 6 males) (Table 6). With one exception, intersyllable interval and duration of the second syllable were again the parameters with the greatest contribution into discrimination. Like the successive approach, cross-validation analyses of the calls recorded in the following year, performed using discrimination cues calculated for pooled call samples of the previous years, showed remarkable decrease of assignment scores (Table 6).

Comparison of these two approaches showed that their results were the similar. However, cumulative approach resulted in somewhat higher correct assignment scores than successive approach. This effect was observed both for average values of between-year classification and for individual scores. For example, calls of male No. 41 showed 35.7 % correct assignment for 1989–1988 between-year classification and 64.3 % correct assignment for 1989–1985 + 1986 + 1987 + 1988 between-pooled-year classification (Tables 5, 6). It is possible, that such differences were conditioned by the fact that, with the same number of individuals, the samples for calculation of within-year classification values were always smaller than those for calculation of pooled-year classification values. It is due to the effect that the larger number of individual calls included into discriminant analysis provides better estimation of their individual variability.

It is evident from Tables 5 and 6, that, for some males, correct assignment values on the base of between-year and between-pooled-year classifications were fairly high from year to year. For example, correct assignment of male No.1 calls resulting from cross-validation analyses was always high and varied from 46.5 % (1987–1986 between-year classification, Table 5) to 78.3 % (1989–1985 + 1986 + 1987 + 1988 between-pooled-year classification, Table 6). The same pattern is evident in males No.5, No.8, and partly, in male No.4, for which only data for the limited period are available. On the other hand, cross-validation correct assignment values for male No.7 had never exceed 36.1 % (1988–1985 + 1986 + 1987 between-pooled-year classification, Table 6) and sometimes declined to 0 % (1987–1986 between-year classification, Table 5). Thus, calls of individual males did differ in their capacity to be classified in the next year with cross-validation analysis.

DISCUSSION

Comparison of the degrees of individual and sexual differences of the loud two-syllable calls of red-breasted geese

Our data for the red-breasted geese showed that the individual differences in two-syllable calls were well expressed, whereas the sexual differences nearly lacked.

In captivity, red-breasted geese use two-syllable calls mainly in spring, in the period of reestablishment of the former and formation of new pair bonds after the period of winter inactivity. These calls were produced during self-advertisement displays and during call-overs among pair mates having lost visual contact to each other (Volodin, 1990b; 1990c). In nature, these calls were reported also as mobbing calls directed to humans, dogs, and Arctic foxes approaching the breeding colony (S.P. Kharitonov, J.I. Kokorev, J.L. Quinn, pers. comm.). Therefore, two-syllable calls proved their function as long-distant vocalisations.

The presence of individual features in long-distant calls should have an important adaptive significance, providing to conspecifics a possibility to recognize their social mates distantly and to change their behaviour adequately depending on the caller's personality. Importance of individual cues was confirmed by many playback studies, e.g. for black-legged kittiwake *Larus tridactylus* (Wooller, 1978), bobwhite *Colinus virginianus* (Baker, Bailey, 1987), great tit *Parus major* (Weary, Krebs, 1992; Lind et al., 1996), black-capped chickadee *Parus atricapillus* (Miyasato, Baker, 1999), black-headed gull *Larus ridibundus* (Charrier et al., 2001), king penguin *Aptenodytes patagonicus* and emperor penguin *A. forsteri* (Aubin et al., 2000; Lengagne et al., 2001; Aubin, Jouventin, 2002), etc.

Compared to individual, sexual differences were poorly expressed and did not allow the discriminant analysis-based geese sexing. It seems that two-syllable calls lack reliable cues to sex, and that sex recognition in the red-breasted geese is based on the other acoustical and locomotory characteristics. In spring, males show much greater activity in initiation of various interactions, than females (Volodin, 1990a). Occasionally, we registered mistakes in sex recognition resulted in formation of male-male pairs in cases when low-rank males with low social activity were present in a group. The male-male pairs included one active and one passive male

(Volodin, 1990a). Another sex-specific peculiarity was that only male red-breasted geese produced loud calls of another type, 'one-syllable calls', during self-advertisement display in horizontal posture. In contrast, female geese adopted this posture only during triumph ceremony, accompanying it with female-specific triumph calls (Volodin, 1990b, 1990c). As regards the two-syllable calls, female geese produced them considerably rarely, and in other situations than males (Volodin, 1990c).

In spite of the fact that discrimination results did not differ from random assignment to sex (Table 4), ANOVA showed significantly higher frequency of maximum amplitude for male in comparison with female calls (Table 3). This result is unusual, because the female body weight equaled no more than 87 % of the male one throughout a year (Volodin, 1992), and one could expect that the larger males have longer vocal tract, providing lower frequencies of maximum amplitude (Fitch, Hauser, 2002). On the other hand, the lower female frequencies of maximum amplitude in two-syllable calls may be related not to the vocal tract resonances, but directly to the functioning of sound source (syrinx), because previous data for the other call types showed that mean female fundamental frequency was lower than the male one. For example, male one-syllable calls recorded during triumph ceremonies in this species showed nearly twofold higher fundamental frequency (1.91 ± 0.03, n = 40), than female triumph-calls (1.10 ± 0.04, n = 22) (Volodin, 1990c). Similar sex differences were showed also for mate-mate alarm duetting in the white-fronted geese *Anser albifrons* (Krechmar, 2003). These data allow us to assume that the red-breasted geese have certain sex-related anatomical structures of the vocal apparatus determining higher fundamental and/or maximum amplitude frequencies in the larger sex (Johnsgard, 1961; Fitch, 1999).

Reliability of individual identification in male two-syllable calls and possibility of bioacoustical monitoring of red-breasted geese in the wild

Our data suggest that individual features of male two-syllable calls remained stable over years. It is indicated by the fact that identification of the caller by its calls in the next year with discriminant analysis was high enough, regardless the approach being applied (successive or cumulative). On the other hand, calls of some individuals (for example, male No.7) had no reliable cues allowing their correct discrimination in the entire call sample in the next year.

The most important for encoding individuality were temporal parameters, such as intersyllable interval and duration of the second syllable. These two parameters showed the highest individual variability (Table 1). The intersyllable interval and duration of the second syllable made the greatest contribution into the individual discrimination both in the entire five-year male-female call sample and in within-year male samples. These temporal parameters were also essential for discrimination rate of the calls through years. Prominent differences in temporal parameters are evident even if the spectrogram patterns are visually compared (Fig. 2).

Large number of power parameters (50 of 55 used in the present study) did not provide the expected effect for individual discrimination. It could be related to strong dependence of power parameters on the distance to the caller, its orientation (angle) to microphone, and masking noise, whereas temporal parameters are much more stable to these factors (Wiley, Richards, 1978; Owings, Morton, 1998; Frommolt, Gebler, 2004). We can expect that another parameter encoding individuality in red-breasted geese might be an interval between entire two-syllable calls produced in bouts. Red-breasted geese almost always produce two-syllable calls in long bouts (Volodin, 1990c), but in the present study we recorded calls in dense flocks and could not register reliably intercall intervals in the individual call bouts. However, it would not be a problem for recording in the wild, because of the small number of nesting pairs in the colonies (Quinn et al., 2003; Kharitonov et al., 2005). Thus, the contribution of intercall interval into individual identification of red-breasted geese and its stability through years should be revealed in the further investigations.

In conditions of high air turbulence, one of the ways of enhancing sound propagation ability is joining calls in series, and further in bouts (Никольский, 1984). In the case of red-breasted goose, nesting in the open windy areas in tundra, provoked the rise of call pattern of two syllables and further formation of the bouts of two-syllable calls. The binary structure of two-syllable call could enhance its propagation ability. Simultaneously, the binary structure provides the best parameter for individual encoding (intersyllable interval) showing the largest individual variability.

Our data suggest the principal possibility of bioacoustical monitoring of the red-breasted geese on the basis of individually distinguishable and relatively sustainable two-syllable calls. The temporal call parameters appeared to be the most important for individual discrimination and supporting call stability over the years. However, final conclusion concerning applicability of this method could be drawn only after it is tested in the wild.

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МОДЕЛИРОВАНИЕ МНОГОЛЕТНЕГО БИОАКУСТИЧЕСКОГО МОНИТОРИНГА НА ПОПУЛЯЦИИ КРАСНОЗОБЫХ КАЗАРОК В НЕВОЛЕ

И. А. Володин[1,2], А. В. Кленова[1], Е. В. Володина[2]

[1] Московский государственный университет им. М. В. Ломоносова, г. Москва, Россия; *volodinsvoc@mail.ru*
[2] Московский зоопарк, г. Москва, Россия

РЕЗЮМЕ

Одно из актуальных направлений в биоакустике связано с разработкой метода индивидуального акустического мониторинга редких видов птиц. Для отслеживания птиц по голосу необходимо, во-первых, обнаружить индивидуальные различия в звуках представителей данного вида и, во-вторых, оценить стабильность обнаруженных различий от года к году. Индивидуальные различия обнаружены в звуках многих видов млекопитающих и птиц, однако лишь в немногих работах исследовали стабильность индивидуальных признаков от года к году, причем данные этих исследований противоречивы. Между тем, если индивидуальные особенности в криках действительно существуют и сохраняются на протяжении всей жизни птицы, то

возможно надёжно отличать её от всех прочих, не производя отловов, мечения и других стрессирующих процедур. Таким образом, акустический мониторинг может в ряде случаев заменить традиционные способы индивидуального прослеживания птиц (в частности, кольцевание) и позволить более подробно исследовать некоторые черты биологии малоизученных видов. Для птиц без внешнего полового диморфизма актуальной также является проблема определения пола по крикам. Такая информация может быть использована как при учёте полового состава диких популяций, так и для бесконтактного определения пола птиц в неволе.

Объектом нашего исследования была краснозобая казарка. Проблема бесконтактного мониторинга очень актуальна для этого вида, гнездовой ареал которого ограничен исключительно территорией России, а численность в природе нестабильна. Самцы и самки краснозобых казарок неразличимы по окраске и почти не отличаются по размерам. В гнездовой период определить пол этих птиц несложно по их поведению, но в другое время сделать это без отлова практически невозможно. Краснозобые казарки гнездятся малыми колониями по 3–10 пар по берегам северных рек. В течение всего репродуктивного сезона самцы размножающихся пар регулярно издают громкие двухударные крики, используя их при окрикивании людей, домашних собак и песцов. Эти крики легко записать в природе, а малые размеры колоний позволяют надёжно идентифицировать кричащую особь.

Целью нашего исследования было сопоставить выраженность индивидуальных и половых различий в громких двухударных криках краснозобых казарок, определить надёжность индивидуальной идентификации в течение нескольких лет и оценить возможность акустического мониторинга для этого вида в природе.

В Московском зоопарке в течение пяти репродуктивных сезонов, с 1985 по 1989 гг., были записаны и проанализированы 1328 громких двухударных криков от 36 краснозобых казарок (22 самцов и 14 самок). В каждом крике измеряли 55 временных и энергетических параметров: длительности первого и второго слогов и интервала между ними, а также по 26 энергетических параметров для каждого из слогов крика. Для того чтобы по набору признаков определить, принадлежит ли записанный крик данной особи или данному полу, использовали процедуру пошагового дискриминантного анализа.

Индивидуальные различия в криках оказались выражены очень ярко. Средняя величина правильного причисления криков к данной особи составила 85,6 % (n = 430 криков от 22 птиц; по 16–20 криков от птицы, выбранных по всем 5 годам), что было достоверно выше случайной величины (14,7 %), рассчитанной на основе процедуры рандомизации. Наибольший вклад в дискриминацию вносили временные параметры: межслоговый интервал и длительность второго слога. Половые различия в двухударных криках казарок практически отсутствовали. Средняя величина правильного причисления криков к данному полу составила 87,2 % (n = 125 криков; по 3 крика от 22 самцов и по 4–5 криков от 12 самок, выбранных по всем 5 годам), что не отличалось от случайной величины, рассчитанной на основе процедуры рандомизации (79,2 %). Вероятно, определение пола у этого вида основано на других поведенческих или акустических ключах. Вместе с тем, частоты максимальной амплитуды каждого из слогов двухударных криков самок оказались достоверно ниже, чем у самцов ($p < 0.001$, ANOVA). Это неожиданно, поскольку обычно более крупный пол производит более низкочастотные звуки, а у краснозобых казарок самцы в среднем крупнее самок.

Стабильность индивидуальных различий в криках самцов была протестирована с помощью процедуры кроссвалидации, при которой рассчитанные на основе одной выборки дискриминантные функции используются для классификации другой выборки. Для этого мы применили два подхода: (1) функции, рассчитанные для криков предшествующей весны, были использованы для классификации криков следующей весны (последовательный подход); (2) функции, рассчитанные для криков нескольких предшествующих вёсен, были использованы для классификации криков следующей весны (накопительный подход).

Внутри каждой из вёсен надежность индивидуальной идентификации птиц по их крикам была очень высокой, и средняя величина не опускалась ниже 82,5 %. Как и для объединенной выборки, наибольший вклад в индивидуальную дискриминацию вносили межслоговый интервал и длительность второго слога. Однако при определении индивидуальной принадлежности криков следующей весны с помощью процедуры кроссвалидации средние величины правильной классификации существенно снижались. При сравнении двух подходов было обнаружено, что при накопительном способе классификации величины правильного причисления оказались несколько выше, чем при последовательном. Таким образом, большее число включённых в анализ криков от каждой птицы способствовало улучшению результатов кросвалидационного анализа.

Кроме этого, были обнаружены сильные индивидуальные различия в стабильности криков год от года. Для четырёх самцов было показано, что двухударные крики надёжно выделяли их из общей выборки с вероятностью от 46,5 до 100 % (в среднем около 70 %). Для одного самца, наоборот, правильность определения криков на следующий год не поднималась выше 36,1 % и обычно составляла около 10 %.

Полученные в нашем исследовании результаты показывают принципиальную возможность акустического мониторинга краснозобых казарок в природе на основе индивидуально различимых и относительно стабильных год от года двухударных криков. Однако окончательно подтвердить возможность его применения может только тестирование в полевых условиях.