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Individual and sexual differences in the calls of the monomorphic White-faced Whistling Duck *Dendrocygna viduata*

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Abstract. The White-faced Whistling Duck is a waterfowl species lacking any differences in ornamentation, coloration, size or behavior between the sexes. For distant communication, this species uses loud whistles. We analyzed 12 spectral parameters of 344 whistles from 23 captive adult ducks (14 males and 9 females). Discriminant analysis showed 94% correct assignment to an individual (N = 279 calls from 14 birds; 15–22 calls per bird). Separately for 8 males (162 calls) and for 6 females (117 calls), discriminant analysis showed 99% and 93% correct assignment to individuals respectively. Discriminant analysis for sex (N = 86; 3 calls from each of 14 males and 5 calls from each of 9 females) showed 100% correct assignment. Intersexual differences were governed by frequency parameters, the values of which were significantly higher in females than in males. Cluster analysis showed that differences between sexes were expressed significantly more strongly than the individual differences. The fact that the "acoustical keys" differed as regards the identification of individual birds or their sex may significantly enhance the reliability of acoustical recognition systems in the White-faced Whistling Duck. The data are discussed in the context of the biology of the White-faced Whistling Duck and significant intersexual differences in syringial and tracheal anatomy, which may be responsible for the sharp distinctions between the sexes in the calls of this species.

Key words: White-faced Whistling Duck, *Dendrocygna viduata*, vocalization, individual differences, sexual differences

INTRODUCTION

In contrast to mammals, whose individual and sexual recognition is based primarily on olfactory stimuli (Bradbury & Vehrencamp 1998), birds identify sex and identity of conspecifics mostly by visual and acoustical performances. Absence of differences in external features and motion behaviour should impose main problem of sexual and individual identification on the acoustic communication channel (Falls 1982, Carlson & Trost 1992, Aubin et al. 2000).

At the beginning of the reproductive season, monomorphic birds must solve two problems: first, to recognize sex of other group members, and, second, after establishing a pair bond, reliably identify the mate among other birds. Acoustic behaviour may play the role of "visiting card"

in monomorphic species, reliably marking sex and individuality. Individual and sexual differences in call structures were discovered in many monomorphic bird species (e. g. Schwanke & Rutschke 1988, Hausberger et al. 1991, Carlson & Trost 1992, Nuechterlein & Buitron 1992, Allenbacher et al. 1995, Mathevon 1996, Ballintijn & ten Cate, 1997, Guyomarc'h et al. 1998, May 1998, Charrier et al. 2001a, etc.). Numerous playback experiments confirmed that responses to the calls of familiar individuals (mates, parents and offsprings) did differ significantly from responses to the calls of unfamiliar birds (e. g. Baker & Bailey 1987, Clapperton 1987, Jones et al. 1987, Jouventin et al. 1999, Aubin et al. 2000, Charrier et al. 2001b, Lengagne et al. 2001, etc.).

As in monomorphic species the same vocalizations may determine both sexual and individual

identity of a caller (Cavanagh & Ritchison 1987, ten Cate 1992, Farquhar 1993, Ballintijn & ten Cate 1997), the question arises what parameters are more responsible for sexual and what parameters — for individual recognition in calls. Another aspect is the expression of sexual and individual differences within a call type — if sexual differences exceed the individual ones or vice versa.

The object of this study is the White-faced Whistling Duck *Dendrocygna viduata*, which is one of the eight anatid species forming the tribe Dendrocygnini — a compact group of waterfowl that lacks sexual dimorphism both in weight and in coloration, as well as in behaviour (Johnsgard 1965, Petrie & Rogers 1997a). Outside the reproductive season, the birds form flocks of 10 to 50 individuals (Petrie & Petrie 1998). At the beginning of the reproductive period, coinciding with the rainy season, the ducks form pairs, leave the flock and establish their nesting territory. Nests are concealed in high grass cover and are sometimes situated close to each other (minimum reported distance between nests was 75 m), but nesting territories do not overlap (Clark 1976). Male and female incubate alternately, and the free partner rests at the edge of the nesting territory and defends it from conspecifics. After hatching, both parents together escort their brood to the nearest reservoir. One parent accompanies the chicks while the other patrols the air; from time to time the partners exchange roles. When the ducklings acquire the ability to fly, the parents lead them to larger bodies of water, where different families gather to form flocks. The families maintain integrity inside the flock and display aggression towards strange families, which disappears some time later (C. Wintle, P. Ginn, pers. comm.). Therefore, personal relations between mates exist at least throughout one reproductive season and some time longer. Altogether, there are no peculiarities, either in adult or young individuals, that allow sexual identification from a distance, except for observation of copulation (Clark 1978, Petrie & Rogers 1997a). Some differences in mates before egg-laying in comfort behaviour (higher in females) and alertness (higher in males) cannot serve as reliable indicators of sex (Petrie & Rogers 1997b).

Whistling Ducks received their name for their characteristic species-specific loud whistling calls (Johnsgard 1965, 1971, Clark 1978). Birds usually produce these calls during foraging and flying in flocks that they form after breeding. Individuals stimulate one another to call, and sometimes all the members of the flock begin to call together (Clark 1978). Besides the loud whistles, the vocal repertoire includes a few other call types, significantly less intensive (Clark 1978, Volodina & Volodin 2003).

The manner of use, extreme loudness and very complex structure in comparison with other call types suggest that just the loud whistles of White-faced Whistling Ducks may be used for long-distant communication between pair or group mates and bear information concerning sexual and individual identity in this monomorphic species. In this study, we conduct multidimensional analysis of individual and sexual differences in the loud whistle structures, determine what parameters are responsible for the individual and intersexual differences, and compare the degrees of individual and intersexual differences of the loud whistles.

METHODS

Studied birds

Twenty three adult White-faced Whistling Ducks (9 males and 2 females from Moscow Zoo and 5 males and 7 females from Tierpark-Berlin) were used as object animals. Their sex was determined before the beginning of the study by cloaca inspection. All birds were individually marked with colored leg rings. In each zoo the ducks were housed in a flock, together with other waterfowl, in an outdoor enclosure with a pool.

Recordings

In Moscow Zoo, loud whistles were recorded from 10 June to 17 September 2001 in the evening after the closure of the zoo for visitors. We made 14 recording sessions, each one was lasting from 25 to 60 min (total 615 min). In Tierpark-Berlin, recordings were made from 18 to 24 September 2003 during the light time. We made 8 recording sessions, each one was lasting from 35 to 135 min (total 665 min). We used tape recorders Agidel-302C or Sony-WM-D6C with dynamic cardioid microphone Tesla-AMD-411N. Both the systems had flat response below 12 kHz. During the recordings, two observers outside the enclosure were determining what individual was producing the loud whistles. Distance from birds to the microphone varied from 2 to 20 m.

Loud whistles were often produced by birds after losing visual contact with conspecifics, and this situation in turn, evoked responses by loud

whistles from conspecifics. The calls were usually produced in series. We did not find any other factors influencing production of loud whistles by this species.

Call analysis

For analysis, we selected calls of good quality, for which individual identity was confirmed by both observers. From birds with more than 20 recorded calls (5 males and 2 females from Moscow Zoo, 1 male and 2 females from Tierpark-Berlin), we selected randomly from 20 to 22 calls per bird. For birds that provided less than 20 calls (4 males from Moscow Zoo, 4 males and 5 females from Tierpark-Berlin), all the calls were included into analysis. In total, we analysed 344 calls, from 4 to 22 calls per individual.

Records were digitized (22 kHz sampling rate, 16 bit precision) using software package Avisoft-SASLab Pro v. 4.2 (© R. Specht). Spectrograms were computed with Hamming window, FFT-length 512 points, frame 50%, overlap 87.5%. These settings provided bandwidth 111 Hz, time resolution 2.9 ms and frequency resolution 43 Hz. The loud whistles of White-faced Whistling

Ducks are tonal, with well-developed harmonics, frequency modulated, and have specific three-part structure (Fig. 1). Throughout a call, three maxima and two minima of fundamental frequency are easy to distinguish. With screen cursor, we measured seven parameters of fundamental frequency: initial frequency (*fini*), end frequency (*fend*), three maxima (*fmax1, fmax2, fmax3*) and two minima (*fmin1, fmin2*) for each call. Five temporal parameters were calculated accordingly to points of frequency parameters measurements: durations of first, second and third parts of a call (*dur1, dur2* and *dur3* respectively), durations between first and second (*dur4*) and second and third (*dur5*) frequency maxima (Fig. 1).

Statistical analysis

We used the discriminant analysis stepwise procedure to determine whether the calls could be assigned to the correct caller or to the correct sex. We have formed two distinct data sets, both with equal sample sizes, for the discrimination to individuality and to sex. The analysis of individual assignment was made for 8 males and 6 females with from 15 to 22 calls per individual
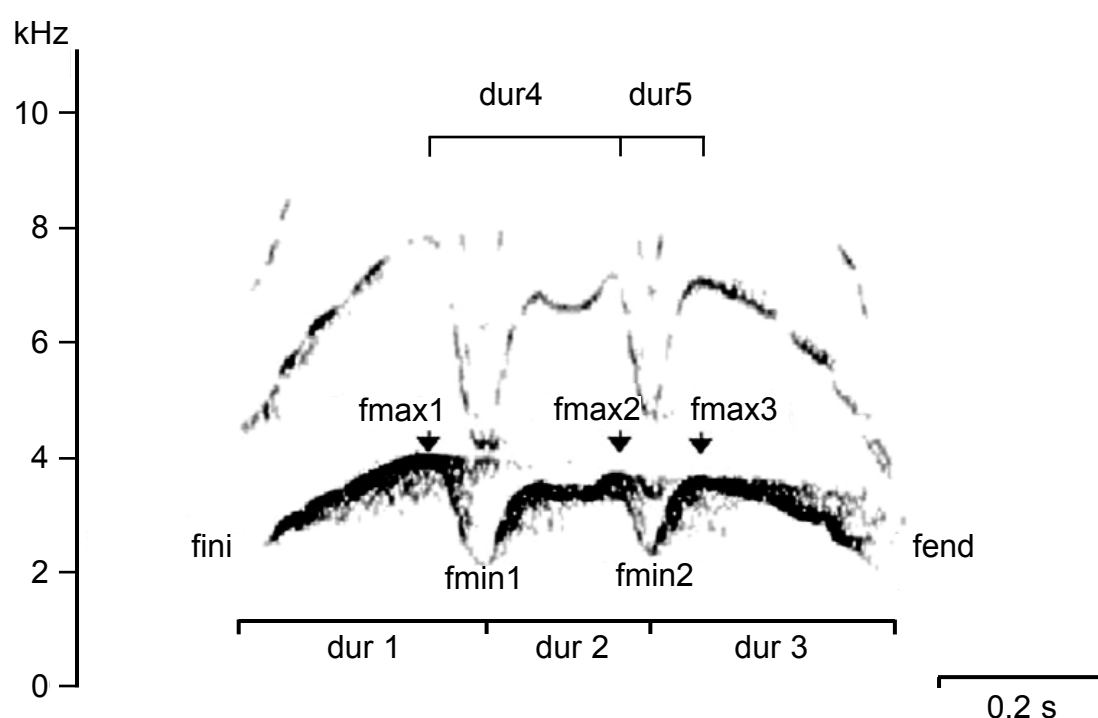
Fig. 1. Measured parameters of loud whistles in the White-faced Whistling Duck. On the spectrogram points of measurements for initial frequency (*fini*), end frequency (*fend*), three maxima (*fmax1, fmax2, fmax3*) and two minima of fundamental frequency (*fmin1, fmin2*) are shown. Sections illustrate measurements of temporal parameters: durations of first, second and third parts of a call (*dur1, dur2* and *dur3* respectively), durations between first and second (*dur4*) and second and third (*dur5*) frequency maxima.

(total 279 calls). Sex assignment was analysed for 14 males (with 3 randomly selected calls per male) and for 9 females (with 5 randomly selected calls per female for 8 females and 4 calls for the ninth one), total — 86 calls, 42 from males and 44 from females. These calls were used as a training set for the subsequent cross-validation procedure. The rest 258 calls (169 male and 89 female calls), not included into discriminant analysis, made up the testing set for the cross-validation procedure.

We used a nested design of ANOVA with an individual nested within sex (with sex — fixed factor and individual — random factor) to compare variability of 12 parameters within and between individuals and to control for possible influences of individual peculiarities on sexual differences in calls. In addition, we performed unweighted average linkage cluster analysis on mean values of 12 frequency and temporal parameters in order to confront data on individual and sexual differences in the loud whistles. All the analyses were made using STATISTICA software package, version 6.0.

RESULTS

Individual differences

ANOVA showed highly significant individual differences for all frequency and temporal parameters of loud whistles (Table 1). Average values of these parameters for 14 individual White-faced Whistling Ducks are given in an Appendix. Individual differences in structure of loud whistles are also evident from spectrograms. Fig. 2 represents spectrograms of loud whistles from four male and four female ducks included into the analysis for individual variability. In spite of considerable similarity in common call pattern (especially within each sex), numerous details (values of frequency maxima and minima, relative duration of call parts etc.) allow to distinguish the calls of one individual from calls of another.

From 15 to 22 calls per individual, for eleven males and six females (279 calls in total), were included into the discriminant analysis for individual differences. Table 2 shows the percentage of correct assignments of loud whistles to

Table 1. Results of nested design ANOVA for individual and sexual differences, with individual nested in sex (with sex — fixed factor, and individual — random factor), and frequency and temporal parameters values (mean ± SD, min–max) of the loud whistle for 14 males and 9 females of White-faced Whistling Ducks.

Call parameters	Nested ANOVA, individual nested in sex		Parameter values for each sex (mean ± SD, min–max)	
	Individual differences	Sexual differences	Male calls (N = 211)	Female calls (N = 133)
fini. kHz	F = 14	F = 1527	2.25 ± 0.13	3.38 ± 0.41
	p < 0.001	p < 0.001	1.96–2.65	2.67–4.69
fmax1. kHz	F = 10	F = 3855	3.97 ± 0.26	6.84 ± 0.65
	p < 0.001	p < 0.001	3.19–4.48	5.24–8.70
fmin1. kHz	F = 15	F = 3203	2.08 ± 0.16	3.19 ± 0.23
	p < 0.001	p < 0.001	1.77–2.71	2.58–3.70
fmax2. kHz	F = 24	F = 3550	3.71 ± 0.27	6.35 ± 0.78
	p < 0.001	p < 0.001	2.93–4.22	4.39–7.75
fmin2. kHz	F = 22	F = 2423	2.31 ± 0.16	3.25 ± 0.28
	p < 0.001	p < 0.001	1.94–2.63	2.63–4.18
fmax3. kHz	F = 32	F = 1580	3.49 ± 0.29	4.77 ± 0.62
	p < 0.001	p < 0.001	2.50–3.98	3.70–7.02
fend. kHz	F = 13	F = 846	1.92 ± 0.19	2.55 ± 0.25
	p < 0.001	p < 0.001	1.16–2.56	2.02–3.36
dur1. ms	F = 36	F = 1322	259 ± 29	171 ± 36
	p < 0.001	p < 0.001	180–325	90–235
dur2. ms	F = 18	F = 573	192 ± 16	153 ± 17
	p < 0.001	p < 0.001	122–232	119–194
dur3. ms	F = 43	F = 8	302 ± 88	269 ± 121
	p < 0.001	p < 0.01	148–523	84–644
dur4. ms	F = 18	F = 234	202 ± 30	163 ± 26
	p < 0.001	p < 0.001	122–253	104–223
dur5. ms	F = 17	F = 3	128 ± 28	120 ± 27
	p < 0.001	p > 0.05	84–224	78–197

Table 2. Assignment of loud whistles to each of 14 White-faced Whistling Duck individuals on the base of discriminant analysis.

Individual	N calls	Correctly classified (%)
male m1	21	95.2
male m3	20	100.0
male m4	18	83.3
male m5	21	81.0
male m6	22	100.0
male m7	18	94.4
male m8	20	100.0
male b3	22	100.0
female m10	22	86.4
female m11	20	100.0
female b6	20	95.0
female b8	21	85.7
female b9	15	93.3
female b11	19	100.0
Total	279	93.9

individual based on the discriminant analysis with the use of 12 frequency and temporal parameters. The average value of correct assignment was 93.9%, that significantly exceeds the random value that is about 7.1% for 14 birds. Individual scores of correct assignment vary from 80.1 to 100%, suggesting that all birds without exception may be reliably discriminated from total sample (Table 1). Stepwise discriminant analysis showed, that three parameters, in order of decreasing importance, have mainly contributed to discrimination to individuality: frequency of first minimum (*fmin1*) and two temporal parameters: *dur3* and *dur1*.

Because female calls did differ considerably in their structure from male ones (Fig. 2), we also conducted discriminant analysis for individual assignment separately for each sex. The discriminant analysis on individual identity done for 8 males (totally 162 calls) showed 98.8% correct assignment (only 2 calls were incorrectly determined). Three parameters, in order of decreasing importance, have mainly contributed to discrimination: frequency of first maximum (*fmax1*), frequency of second minimum (*fmin2*) and frequency of third maximum (*fmax3*). The discriminant analysis for individual identity done for six females (totally 117 calls) showed 93.2% correct assignment with major contribution to discrimination of temporal parameters *dur3*, *dur1* and *dur2*.

Sexual differences

It was found that values of all frequency parameters of female calls were considerably and significantly higher than those of male calls, with lack of overlapping of samples for three parameters (*fini*, *fmax1* and *fmax2*). Dif-
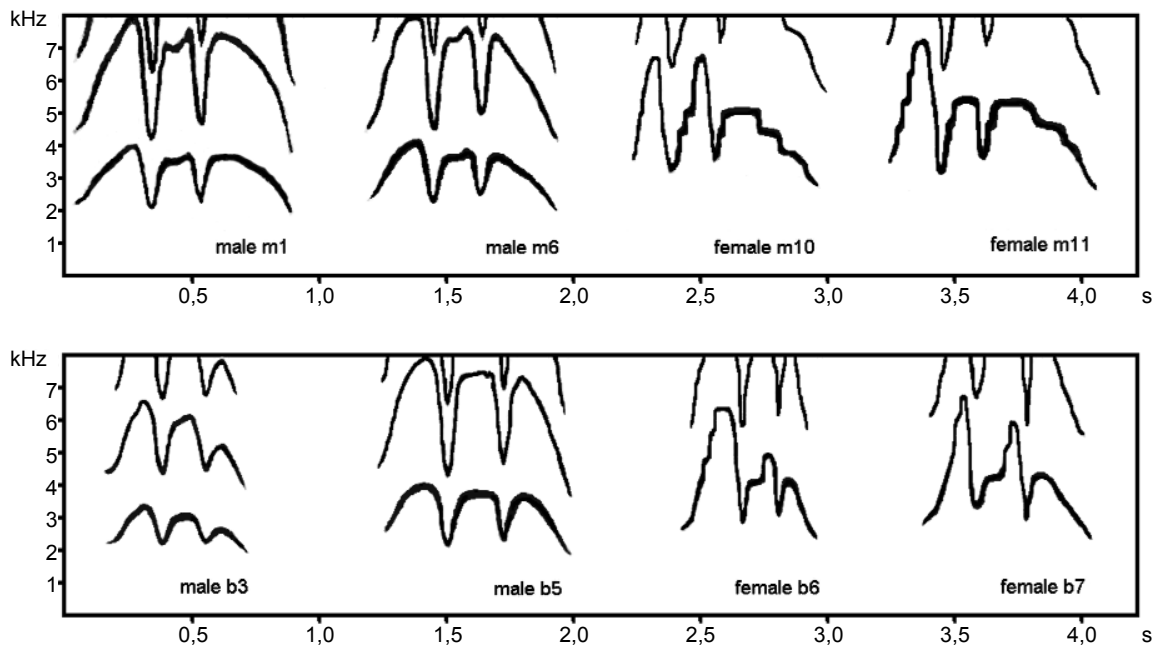

Fig. 2. Spectrograms illustrate loud whistles of four male (m1, m6, b3 and b4) and four female (m10, m11, b6 and b7) White-faced Whistling Ducks. The letter codes m and b denote affiliation of birds to Moscow Zoo and Tierpark Berlin respectively.

Table 3. Assignment of male and female loud whistles of the White-faced Whistling Duck to a certain sex on the base of discriminant analysis and data of cross-validation analysis with use of counted discriminate functions for calls not included into discriminant analysis.

Actual group	Predicted group membership		Total	Correctly classified (%)
	Males	Females		
Discriminant analysis				
Males	42	0	42	100.0
Females	0	44	44	100.0
Total	42	44	86	100.0
Cross-validation analysis				
Males	169	0	169	100.0
Females	0	89	89	100.0
Total	169	89	258	100.0

ferences between values of temporal parameters were expressed less strongly: although four of five averages were significantly higher in males, male and female samples overlapped in all duration measures in much more extent than those of frequency parameters (Table 1).

Three randomly selected calls from each of 14 males and five randomly selected calls from each of 9 females were included into analysis for sexual differences. The discriminant analysis for sex with use of 12 frequency and temporal parameters showed 100% correct assignment (Table 3). Stepwise procedure revealed that *fmax1*, *fmin1* and *dur1* have mainly contributed to discrimination to sex. The including into the analysis of just two frequency parameters (*fmax1* and *fmin1*) provided 100% correct assignment to sex. The cross-validation procedure, applied with use of 258 calls that were not included into discriminant analysis (169 male and 89 female calls), also showed 100% correct assignment to sex (Table 3).

Distribution of values for first frequency maximum (*fmax1*) illustrates fairly expressed intersexual differences in call structure in the White-faced Whistling Duck (Table 1). This variable is one of three parameters with non-overlapping measurements for male and female call samples. In addition, it introduces the most important contribution into discrimination between sexes; this variable alone is sufficient for reliable sexing in this duck species.
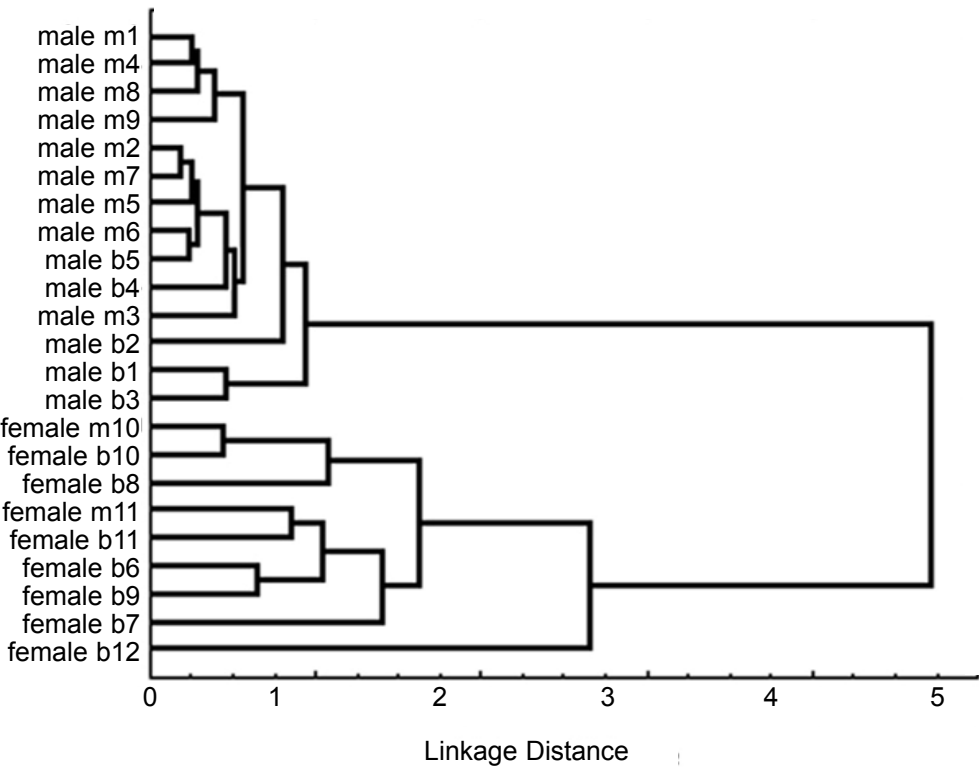

Fig. 3. The unweighted average linkage clusterogram, illustrating similarity in loud whistles of 23 White-faced Whistling Duck individuals. Note that intersexual differences exceed significantly differences within sexes.

Comparison of individual and intersexual differences

The unweighted average linkage clusterogram shows correspondence among individual and sexual differences in loud whistles of the White-faced Whistling Ducks (Fig. 3). It is obvious that differences between sexes are expressed more clearly in comparison with individual differences. However, although being relatively "small", these individual differences already provide more than 98% probability for individual identification among males and more than 93% probability among females. In addition, the received data provided evidence that calls of birds of the same sex from different zoos were much more close to each other in their structures, than with calls of opposite sex from the same zoo. Moreover, calls of birds of the same sex do not cluster with each other by their affiliation to a certain zoo, and calls of birds from different institutions may be more similar, than calls of birds from the same zoo.

DISCUSSION

Our data suggest that loud whistles of the White-faced Whistling Duck provide reliable characteristics for sexual and individual identification. Loud whistles of whistling ducks have a number of peculiarities, distinguishing them from other call types in their vocal repertoire. First, this is a very complex characteristic of frequency modulation. Calls of other types are either flat or have simple reversed-U-form of modulation (Volodina & Volodin 2003). Moreover, in contrast to other call types, the loud whistles are produced at very high intensity and stimulate other conspecifics to respond by the same calls (Clark 1978, our unpublished data). Altogether, these arguments indicate especial communicative role of loud whistles, and possibility to use them for distant communication in Dendrocygnini.

It seems that the reliable sex and individual recognition should be extremely important for the White-faced Whistling Duck, which is monogamous and territorial during the breeding season, when both sexes share parental duties, including incubation, with change-over at the nest (C. Wintle, P. Ginn, pers. comm.). The possibility of mate recognition by loud whistles from the distance appears to be crucial because these birds make their nest well concealed in high grass (Clark 1976). Many monomorphic bird species with similar reproductive behaviour (guarding a nest territory, nesting in closed habitats and sharing parental care) also use acoustic channels for distant identification of a mate, applying callovers or structurally complex duet singing (Wickler 1976, Farabaugh 1982, Noel & Keulen 1997). Wickler & Seibt (1982) supposed that the evolution of duetting in birds and accompanying acoustical dimorphism may result in disappearing of visible sexual dimorphism.

Absence of differences in coloration and behaviour between sexes in the White-faced Whistling Duck during reproductive period may suggest a lack of sexual selection on these features, as males and females pay equal costs of parental care. Indeed, the behaviour of mates is similar during egg-sitting and brood raising (C. Wintle, P. Ginn pers. comm.) The assumption that mates bear equal costs of incubation is supported also by the fact, that males and females spend equal percentage of time foraging during pre-incubation period. In contrast, in waterfowl of temperate latitudes, only females incubate, and they forage significantly more than males (Petrie & Rogers 1997a, 1997b).

We found that, in spite of well-expressed individual differences in loud whistles of the White-faced Whistling Duck, the sexual differences in voices exceed significantly the individual ones. The individual and sexual identities of loud whistles of the White-faced Whistling Duck are based on different acoustic keys. Complexity of frequency modulation in the loud whistle allows encoding individuality by relative durations of different call parts (primarily in females), as well as variability in frequency maximal and minimal values (primarily in males). Drastic intersexual differences are determined presumably by the fact that male and female calls lie in different, practically non-overlapping frequency ranges. Calls of females are considerably higher in frequency than male calls, the fact that provides the possibility of determining sex even to an unarmed ear. Therefore, structural differences in loud whistles provide White-faced Whistling Ducks with the potential to determine reliably the sex of conspecifics during pairing and to recognise the mate during the breeding period. The fact that "acoustical keys" are different for individual and for sex identification may significantly enhance reliability of acoustical recognition system in the White-faced Whistling Duck.

In other monomorphic non-passerine birds, differences in male and female calls may also depend on both frequency and temporal vocal

parameters. As a rule, intersexual differences in temporal characteristics are related with the number of notes or calls in vocal sequences, with sound/silence ratio in call bouts or with call durations (Cavanagh & Ritchison 1987, Ballintijn & ten Cate 1997).

In most species, male calls are lower in frequency than female calls. For example, it was found in Common Screech-Owl *Otus asio* (Cavanagh & Ritchison 1987), Whooping Crane *Grus americana* (Carlson & Trost 1992), Black-necked Grebe *Podiceps nigricollis* (Nuechterlein & Buitron 1992) and Collared Dove *Streptopelia decaocto* (Ballintijn & ten Cate 1997). In contrast, in White-tailed Hawk *Buteo albicaudatus* (Farquhar 1993) and Leach's Storm-Petrel *Oceanodroma leucorhoa* (Taoka et al. 1989) male calls are higher in frequency, than female calls. As a rule, in these species intersexual differences in frequency do not exceed 25–30%. As distinct from that, in the loud whistle of White-faced Whistling Ducks the female frequency exceed the male frequency more than one and a half.

In most species, the larger sex produces calls lower in frequency, because body size usually correlate with size of syrinx. In the White-faced Whistling Duck, males and females are very close in their weight (Petrie & Rogers 1997a). However, in this species, as well as in other representatives of tribe Dendrocygnini, there are significant intersexual differences in the anatomy of vocal tract. First, males have a rounded symmetrical inflation in the base of trachea — tracheal bulla, whereas females do not have such extension. Second, in females, immediately above the syrinx, low tracheal rings are not closed-loop ventrally, which results in formation of narrow elongate slit, covered with *membrana tracheosyrengialis* (Johnsgard 1961, 1971, Livezey 1995). However, the influence of intersexual differences in vocal anatomy on male and female call structures has not yet been studied. Although the vocal role of these anatomical formations, situated just above voice source, is not clear to date, one likely possibility is that both of them or at least one of them introduce their contribution into strong acoustic sexual dimorphism of loud whistles in the White-faced Whistling Duck.

In case these anatomical influences on call structures were confirmed properly in the future, the White-faced Whistling Duck may be considered as a good example of substitution of external sexual dimorphism for "internal" tracheal dimorphism, representing highly reliable acoustic cues for sex determination in species that lack differences in ornamentation, coloration, size and behaviour between sexes.

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STRESZCZENIE

[Osobnicze i międzypłciowe zróżnicowanie głosów u monomorficznej drzewicy białolicej]

Badano drzewicę białolicą, gatunek ptaka blaszkodziobego z podrodziny Anserinae, charakteryzujący się brakiem dymorfizmu płciowego w ubarwieniu, wielkości ciała czy jakichkolwiek ozdobach. Komunikację długodystansową umożliwia tym ptakom wydawanie niezwykle głośnych gwizdów. Przeanalizowano 12 parametrów (Fig. 1) charakteryzujących spektrum 344 gwizdów pochodzących od 23 dorosłych osobników żyjących w niewoli (14 samców i 9 samic). W oparciu o analizę wielowymiarową (zagnieżdżona ANOVA, analiza dyskryminacyjna, analiza skupień) pokazano wyraźne osobnicze i płciowe zróżnicowanie wszystkich mierzonych parametrów spektrum i czasowych głosu (Tab. 1). Analiza dyskryminacyjna z 94% skutecznością klasyfikowała badane głosy do poszczególnych osobników (n = 279 głosów od 14 ptaków; 15–22 głosów na osobnika (Tab. 2). Analiza dyskryminacyjna obliczona oddzielnie dla 8 samców (162 głosy) i 6 samic (117 głosów) umożliwiła poprawne przypisanie głosu do osobnika w 99% (samce) i 93% (samice) przypadków. Najistotniejszymi zmiennymi kodującymi odrębność poszczególnych samców były maksymalne i minimalne częstotliwości głosu, podczas gdy samice najbardziej różniły się między sobą stosunkiem czasu trwania poszczególnych części głosu. Analiza dyskryminacyjna mająca na celu rozpoznanie płci osobnika (n = 86; 3 głosy od 14 samców i 5 głosów od każdej z 9 samic) była w 100% skuteczna (Tab. 3). Różnice między płciami dotyczyły głównie parametrów częstotliwości, które były istotnie wyższe u samic niż u samców (Fig. 2). Po zastosowaniu procedury sprawdzającej, w której przeanalizowano 258 głosów nie uwzględnionych we wcześniejszych analizach dyskryminacyjnych (169 głosów samców i 89 głosów samic) stwierdzono 100% poprawne klasyfikowanie głosu do płci (Tab. 3). Analiza skupień wykazała, że różnice

międzypłciowe u badanego gatunku były isto-
tnie większe niż różnice międzyosobnicze
(Fig. 3). Głos u drzewicy białolicej jest więc
rzetelnym sygnałem oznajmiającym płeć oraz
tożsamość osobnika. Wyniki pracy są zgodne z
danymi o anatomii badanego gatunku, u którego

stwierdzono istotne międzypłciowe zróżnico-
wanie krtani dolnej (syrinx) oraz dróg głosowych,
w tym tchawicy. Różnice te są najprawdopo-
dobniej bezpośrednią przyczyną stwierdzonego
dymorfizmu płciowego w głosie drzewicy biało-
licej.

Appendix. Values (mean ± SD) of the loud whistle frequency and temporal parameters for 14 White-faced Whistling Ducks, included into discriminant analysis of individual differences.

Birds	N of calls	Call parameters											
		fini, kHz	fmax1, kHz	fmin1, kHz	fmax2, kHz	fmin2, kHz	fmax3, kHz	fend, kHz	dur1, ms	dur2, ms	dur3, ms	dur4, ms	dur5, ms
male m1	21	2.18± 0.07	3.92± 0.10	1.99± 0.09	3.65± 0.11	2.26± 0.09	3.57± 0.10	1.93± 0.23	296± 18	188± 10	279± 34	212± 17	110± 10
male m3	20	2.45± 0.05	4.24± 0.07	2.14± 0.10	4.06± 0.12	2.47± 0.08	3.75± 0.11	2.20± 0.13	234± 7	189± 7	412± 69	219± 10	138± 22
male m4	18	2.16± 0.11	4.02± 0.19	1.95± 0.06	3.76± 0.27	2.10± 0.10	3.47± 0.17	1.84± 0.14	266± 17	196± 17	325± 76	220± 18	117± 17
male m5	21	2.21± 0.05	4.19± 0.08	2.05± 0.05	3.74± 0.08	2.43± 0.11	3.54 0.15	1.86± 0.10	261 10	191± 7	312± 60	160± 36	154± 32
male m6	22	2.25± 0.14	4.13± 0.07	2.22± 0.06	3.86± 0.06	2.48± 0.05	3.67± 0.05	1.96± 0.15	258± 15	181± 6	294± 17	202± 11	112± 8
male m7	18	2.38± 0.03	4.16± 0.13	1.99± 0.07	3.87± 0.08	2.38± 0.06	3.54± 0.07	1.95± 0.14	232± 30	194± 10	253± 30	215± 15	102± 6
male m8	20	2.17± 0.04	3.86± 0.05	1.93± 0.05	3.70± 0.05	2.09± 0.04	3.66± 0.07	1.78± 0.09	303± 9	203± 6	444± 33	216± 8	122± 6
female m10	22	3.46± 0.24	7.22± 0.36	3.21± 0.17	7.06± 0.40	3.52± 0.23	5.29± 0.39	2.74± 0.22	167± 17	163± 12	433± 85	180± 14	152± 31
female m11	20	3.19± 0.33	6.71± 0.92	2.95± 0.18	6.31± 0.90	3.32± 0.27	5.01± 0.52	2.60± 0.16	206± 10	145± 8	369± 95	173± 23	118± 25
male b3	22	2.16± 0.03	3.47± 0.15	2.16± 0.04	3.18± 0.13	2.24± 0.05	2.90± 0.25	1.89± 0.09	237± 12	184± 8	201± 36	179± 25	140± 31
female b6	20	3.49± 0.30	6.33± 0.37	3.31± 0.19	6.21± 0.28	3.08± 0.18	4.47± 0.37	2.38± 0.16	144± 19	131± 6	190± 32	125± 10	118± 14
female b8	21	3.86± 0.40	6.92± 0.49	3.36± 0.10	6.70± 0.45	3.18± 0.18	4.46± 0.22	2.45± 0.14	125± 33	148± 15	194± 29	149± 18	106± 9
female b9	15	3.09± 0.23	6.34± 0.54	3.20± 0.26	5.80± 0.59	3.00± 0.11	4.22± 0.39	2.27± 0.15	179± 12	171± 17	214± 45	173± 19	116± 12
female b11	19	3.15± 0.18	7.03± 0.45	3.18± 0.12	5.61± 0.28	3.26± 0.12	4.77± 0.18	2.72± 0.28	212± 7	159± 7	191± 19	181± 20	102± 9