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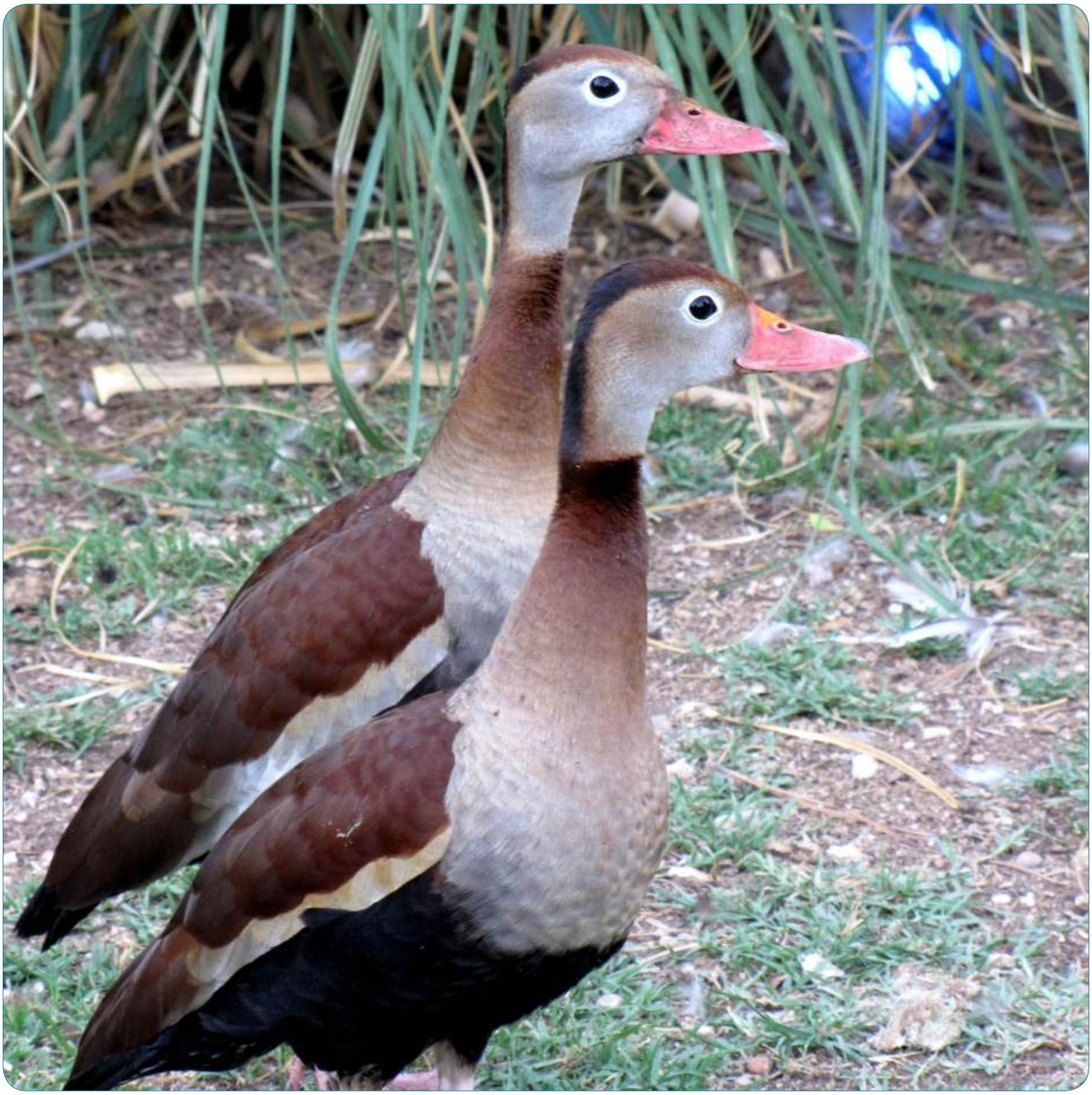

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Volodin *et al.*

BioMed Central

Volodin *et al. Avian Res* (2015) 6:20
DOI 10.1186/s40657-015-0033-y

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REVIEW

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Gender identification using acoustic analysis in birds without external sexual dimorphism

Ilya A. Volodin[1,2*], Elena V. Volodina[2], Anna V. Klenova[1] and Vera A. Matrosova[3]

Abstract

Zoo and wildlife management faces a problem with bird sexing, as many bird taxa have indiscernible gender differences in size and coloration. Problematic groups are geese, cranes, rails, raptors, owls, parrots, doves, auks, shearwaters and some passerines. Commonly accepted invasive sexing techniques based on genetics, laparoscopy, morphometric and on cloacal inspection, are all needed in bird capturing and handling. Capturing and subsequent manipulations may be inapplicable for free-ranging birds, whereas distant voice-based sexing is relevant for many species. This review evaluates the potential for noninvasive sexing by separate calls or duet calls, for adult birds of 69 species from 16 orders and for chicks of 11 species from 7 orders. For adult birds of 25 species, a single call per individual was sufficient for 100 % reliable sexing by ear or using spectrographic analysis. For chicks, the potential for voice-based sexing seems to be very limited. For birds calling rarely or unpredictably, we propose a simple way of provoking vocalization using playbacks of species-specific calls that are available from sound libraries. We conclude that sexing by voice may represent a feasible alternative to the classical sexing techniques, both in the wild and in captivity.

Keywords: Vocalization, Monomorphic birds, Call-based sexing, Sexing by sound

Introduction

Monomorphic birds lack prominent gender differences in body size and feather coloration. Such species are usual in many taxa: among geese, cranes, rails, raptors, owls, parrots, doves, auks, shearwaters and some passerines (e.g. Clapperton 1983; Cavanagh and Ritchison 1987; Carlson and Trost 1992; Ballintijn and ten Cate 1997; Smith and Jones 1997; Venuto et al. 2001; Eda-Fujiwara et al. 2004; Volodin et al. 2005a, 2009; Klenova et al. 2012). Sexing monomorphic birds represents a problem in both captive and wildlife management, e.g., in forming pairs for breeding and estimating sex ratios during censuses.

Commonly applied techniques to sex birds include laparoscopy, cloacal examination, morphometric and genetic analyses. All include capturing birds and employing methods unpleasant for the birds or even painful procedures that impair their welfare. Noninvasive sexing by behavioral displays is accurate only during mating, since courtship displays, nest building, incubation and chick care represent shared duties in pairs of many monomorphic birds and thus do not provide unambiguous indices of sex. In addition, some monomorphic birds form homosexual pairs that are indistinguishable by behavior from heterosexual pairs (Buchanan 1966; Fabricius 1981; Conover and Hunt 1984; Hunt et al. 1984; Conover 1989; Volodin 1990c; Elie et al. 2011).

Laparoscopy is a highly invasive surgery-based method, although its application has no significant effects on survival and body mass of birds in nature (Richner 1989). Cloacal sexing is a broadly applied technique, for it provides immediate results, does not need special equipment and is not traumatic (Volodin et al. 2009; Bazzano et al. 2012). However some authors mention negative effects associated with this technique: traumas (Turner 1953), stress, bleeding (Malagó et al. 2005) as well as prolapses and infections to ratite chicks (Huchzermeyer 1998; Soley and Groenewals 1999). For waterfowl, this

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method includes cloaca inversion (Hanson 1949; Purchase 1978; Volodin et al. 2009), whereas for doves, alcids, penguins and some rails, cloacal sexing is possible by the cloaca orifice, which is prominent in females during the egg laying period (Serventy 1956; Boersma and Davies 1987; Copestake et al. 1988). The reliability of this method varies among species and is reported to be about 90 % for doves (Miller and Wagner 1955; Swanson and Rappole 1992), 90 % for Whistling Ducks (*Dendrocygna* sp.) (Volodin et al. 2009), between 93 and 96 % for shearwaters and petrels (Boersma and Davies 1987; O'Dwyer et al. 2006), 92 % for Magellanic Penguins (*Spheniscus magellanicus*) (Boersma and Davies 1987), 98 % for chicks of the Greater Rhea (*Rhea americana*) (Boersma and Davies 1987) and 100 % for American Coots (*Fulica americana*) (Boersma and Davies 1987).

Morphometric-based sexing relies on measuring small differences in body size between genders. For this sexing technique, discriminant functions based on measuring different body parts should be created, to allow the gender of a particular individual to be determined (Green 1989; Guallar et al. 2010). This sexing technique requires minimal equipment and staff training and provides immediate results. However, the reliability of morphometric sexing is limited: up to 80 % for razorbills *Alca torda* (Grecian et al. 2003), 80 % for Parakeet Auklets (*Cyclorhynchus psitacula*) (Klenova et al. 2012) and 94 % for Crested Auklets (*Aethia cristatella*) (Klenova et al. 2012), 87 % for Yelkouan Shearwaters (*Puffinus yelkouan*) (Bourgeois et al. 2007), 90 % for Balearic Shearwaters *Puffinus mauretanicus* (Genovart et al. 2003), 85 % for Blue-fronted Amazons (*Amazona aestiva*) (Berkunsky et al. 2009), 88 % for Common Wood Pigeons (*Columba palumbus*) (O'Huallachain and Dunne 2010), 95 % for Mute Swans (*Cygnus olor*) (Brown et al. 2003) and 96 % for adult and 90 % for subadult Coscoroba Swans (*Coscoroba coscoroba*) (Calabuig et al. 2011).

Genetically-based sexing is very reliable (Griffiths et al. 1998; Morinha et al. 2012), but relatively expensive and requires a specially equipped laboratory and time for conducting the genetic analyses. This method requires the capture of birds for sampling blood, feather or saliva, although some advanced techniques allow gene samples to be taken from materials obtained noninvasively, such as molt feathers, feces and the inner layer of egg shells (Jensen et al. 2003; Regnaut et al. 2006; Balkiz et al. 2007; Mudrik et al. 2013). However, accurate genetic sexing with noninvasive samples requires highly qualified staff and methods have to be adapted for any particular species (Beja-Pereira et al. 2009). Incorrect settings of genetic analyses may, to some extent, decrease the reliability of the genetic method of sexing.

As an alternative to the commonly used invasive sexing methods, the noninvasive call-based sexing method has proved useful for many monomorphic bird species. This method does not require the capture and manipulation of birds for gene sampling, body measurements, or cloaca inversion and therefore obviates any potential trauma. Sex differences in the voices of monomorphic birds may arise from respective differences in the morphology and size of vocal apparatus between genders (Johnsgard 1961; Livezey 1991, 1995). Otherwise, they may arise from differences in the method of vocal production in males and females with the same construction of vocal apparatus (Niemeier 1979), or from both sex differences in the construction of vocal apparatus and in the method of vocal production (Ballintijn and ten Cate 1997). As well, sex differences can also arise in the type of calls/songs used by males and females and not only in acoustic parameters. Reliability of call-based sexing reaches 100 % for species with strong vocal differences between males and females (e.g. Volodin et al. 2009).

Methods

Acoustic terms and definitions

Sexing monomorphic birds by voice is mainly based on the analysis of computer images of vocalizations (Fig. 1). Spectrograms reflect changes of call frequency characteristic over time and power spectra, reflecting temporal changes in amplitude. The visual analysis of spectrograms and power spectra is much more reliable and unbiased in comparison to sexing by ear, so it is applicable to a broader range of bird species.

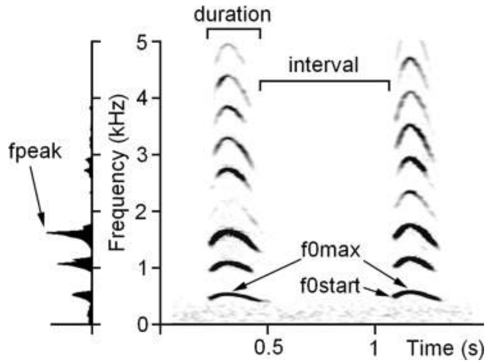

Fig. 1 Acoustic variables that are mostly applied for bird sexing by voice. Spectrogram (*right*) and power spectrum (*left*) of two advertising calls produced by male Magpie Goose (*Anseranas semipalmata*) are given. Designations: *fpeak* the dominant frequency, *duration* the call duration, *interval* the inter-call interval, *f0max* the maximum fundamental frequency, *f0start* the fundamental frequency at the beginning of the call. Calls for this and other illustrations were recorded by the authors

General terms

Call: Bird vocalization, other than learned courtship song in oscines. Song: Courtship or territorial vocalization in oscines, typically uttered by a male songbird in characteristic bursts or phrases. Sound: Acoustic quality perceived by human ear, or used as adjective (e.g. "sound library"). Vocalization: Any kind of acoustic signal, produced by the vocal apparatus of birds (syrinx). Playback: Translation of recorded bird calls or songs to bird recipients and observing/recording their movemental or vocal responses. Note: The smallest unit of vocalization, representing uninterrupted trace on the spectrogram. Syllable: Combination of notes, separated by intervals noticeably shorter than those between syllables. Rhythmic structure: Characterized by the number and repetition rate of notes, syllables or calls. Overlapping ranges of values: Ranges of values of acoustic variables, that are partly or perfectly the same in either sex.

Spectrogram-related acoustic terms

Fundamental frequency: In birds, voice pitch is characterized by the frequency of vibration of the syrengial membranes, or call fundamental frequency (Goller and Riede 2013). This is the fundamental call frequency, measured in Hertz (1 Hz = 1 vibration per second). On the spectrogram the fundamental frequency is usually represented by the lowest band in the stock of integer multiple bands, termed harmonic. The fundamental frequency can be dampened by a bird by altering the structure of the vocal cavity in some cases. The fundamental frequency is the acoustic variable that most often discriminates between the calls of male and female birds. Vegetation and distance do not affect the use of frequencies to discern between genders, as fundamental frequency variables are not affected by these factors (Matrosova et al. 2010). Frequency modulation: Changes in fundamental frequency contour during a call. Harmonics: Integer multiple frequency bands upon the fundamental frequency band. Tonal call: Call, containing the fundamental frequency and its related harmonics. Noisy call: Call where the fundamental frequency and harmonics are indistinguishable or lacking from the inside, more or less uniform noise on the spectrogram. Maximum frequency: This term is scientifically imprecise, so the authors cited may understand it differently. We use this term following the authors of the papers reviewed, because their findings, although insufficiently defined, nevertheless indicate bird species in which sexes can be potentially discriminated by voice.

Power-spectrum-related acoustic terms

Dominant frequency: The frequency, where the maximum energy of a call is concentrated. Amplitude: The relative intensity of calls or call components, evident from degrees of blackening on respective parts of the spectrogram. All power variables can be slightly affected by distance or vegetation cover (Matrosova et al. 2010).

Applicability of sexing by voice

Sexing by voice is primarily applicable for bird species for which this method unambiguously classifies the given individual as a male or a female, i.e., it is 100 % reliable. At non-overlapping values of one or a few acoustical variables between sexes (e.g. when male calls are always higher in pitch than female calls, without exclusions), individuals may be sexed with 100 % reliability. Just visual inspection of spectrogram without measuring the acoustic variables would be sufficient in these cases (e.g. Volodin et al. 2009). However, when acoustic variables overlap between sexes, some individuals may be sexed incorrectly. In this case, the percentage of correct classification to sex may be calculated with discriminate function analysis (DFA). DFA calculates the percentage of correct assignment to sex based on the set of measured acoustic variables introduced into the analysis. Given that the number of groups for classifying sex with DFA is only two (males and females), we consider that a <70 % correct classification would make sexing by voice impossible, 70–80 %—low reliability of sexing, 81–90 %—high but imperfect reliability of sexing and 91–100 %—perfect reliability of sexing.

In the following we review studies and report on vocal features that allow or do not allow reliable discrimination between males and females by their calls for species in which the sexes are practically undistinguishable by external appearance. These studies are presented according to current bird taxonomy (Boyd 2013; Penhallurick 2013). For studies, conducted on adult birds, the number of subjects of each sex is presented in Table 1. For studies, conducted on chicks, the number of subjects of each sex is given in the text.

Sexing adult birds by voice

Order Apterygiformes

In the Little Spotted Kiwi (*Apteryx owenii*), loud whistle calls differ substantially between the sexes (Digby et al. 2013). The average fundamental frequency of males was 1.5 times higher than those of females (2800 and 1800 Hz, respectively). Although these birds have some dimorphism of body size, with males slightly lighter in weight than females (1.2 and 1.4 kg, respectively), distant sexing by far-propagating whistle calls is important for the census of this species in the wild.

Order Anseriformes

Among Anseriformes, sex differences in calls were studied in detail in four species, in which sex differences could

Table 1 Studies of vocal sex dimorphism of monomorphic birds included in this review

Order	Common and scientific names	Call type	Method	Sexing reliability	Number of birds	References
Apterygiformes	Little Spotted Kiwi (*Apteryx owenii*)	Loud whistle call	Measuring acoustic variables	100 %	9 m; 6 f	Digby et al. (2013)
Anseriformes	White-faced Whistling Duck (*Dendrocygna viduata*)	Loud whistle call	Measuring acoustic variables	100 %	14 m; 9 f	Volodin et al. (2005a, 2009)
	Fulvous Whistling Duck (*Dendrocygna bicolor*)	Loud whistle call	Measuring acoustic variables	100 %	6 m; 5 f	Volodin et al. (2009)
	Cuban Whistling Duck (*Dendrocygna arborea*)	Loud whistle call	Measuring acoustic variables	100 %	10 m; 7 f	Volodin et al. (2009)
	Red-billed Whistling Duck (*Dendrocygna autumnalis*)	Loud whistle call	Measuring acoustic variables	100 %	4 m; 4 f	Volodin et al. (2009)
	Red-breasted Goose (*Branta ruficollis*)	Two-syllable call	Measuring acoustic variables and DFA	No sex differences	22 m; 12 f	Volodin et al. (2008)
	Red-breasted Goose (*Branta ruficollis*)	Duet call (triumph ceremony)	Revealing male and female parties by spectrogram	100 %	65 birds	Volodin (1990b)
	White-fronted Goose (*Anser albifrons*)	Duet call (triumph ceremony)	Visual inspection of spectrogram	High	Not given	Krechmar (2003)
Galliformes	Willow Ptarmigan (*Lagopus lagopus*)	"krrow" call	Visual inspection of spectrogram	High	Not given	Martin et al. (1995)
Podicipediformes	Black-necked Grebe (*Podiceps nigricollis*)	Advertising call	Measuring acoustic variables	High	38 m; 27 f	Nuechterlein and Buitron (1992)
Columbiformes	Orange-bellied Fruit-dove (*Ptilinopus iozonus*)	Coo call	Visual inspection of spectrogram	High	Not given	Baptista and Gaunt (1997)
	Eurasian Collared Dove (*Streptopelia decaocto*)	Coo call	Measuring acoustic variables	100 %	9 m; 6 f	Ballintijn and ten Cate (1997)
Caprimulgiformes	Marbled Frogmouth (*Podargus ocellatus*)	Gobble call	Measuring acoustic variables	High	20 m; 21 f	Smith and Jones (1997)
Cuculiformes	Pheasant Coucal (*Centropus phasianinus*	Descending whoops call; scale call	Measuring acoustic variables	High	9 m; 9 f	Maurer et al. (2008)
Gruiformes	Purple Swamphen (*Porphyrio porphyrio*)	Crowing call	Visual inspection of spectrogram	High	Not given	Clapperton (1983)
	American Hoot (*Fulica americana*)	Squeak call, 1-note recognition call, 2-note recognition call	Measuring acoustic variables	100 %	14 birds	Cosens (1981)
	Whooping Crane (*Grus americana*)	Guard call	Measuring acoustic variables and DFA	High	141 m; 118 f	Carlson and Trost (1992)
	White-naped Crane (*Grus vipio*)	Guard call	Measuring acoustic variables	Low	5 m; 5 f	Bragina and Beme (2013)
	White-naped Crane (*Grus vipio*)	Duet call	Revealing male and female parties by spectrogram	100 %	Not given	Swengel (1996)
	Siberian Crane (*Grus leucogeranus*)	Trill call	Measuring acoustic variables	High	9 m; 9 f	Bragina and Beme (2007)
	Red-crowned Crane (*Grus japonensis*)	Duet call	Revealing male and female parties by spectrogram	100 %	10 m; 10 f	Klenova et al. (2008)
Procellariiformes	Leach's Storm-petrel (*Oceanodroma leucorhoa*)	Chatter call	Measuring acoustic variables	100 %	14 m; 12 f	Taoka et al. (1989a)
	Swinhoe's Storm-petrel (*Oceanodroma monorhis*)	Flight call	Visual inspection of spectrogram	100 %	50 m; 50 f	Taoka et al. (1989b), Taoka and Okumura (1990)

Table 1 continued

Order	Common and scientific names	Call type	Method	Sexing reliability	Number of birds	References
	Madeiran Storm-petrel (*Oceanodroma castro*)	Flight call	Visual inspection of spectrogram	100 %	Not given	James and Robertson (1985a)
	Fork-tailed Storm petrel (*Oceanodroma furcata*)	Single-syllable call	Visual inspection of spectrogram	100 %	Not given	Simons (1981)
	Greater Shearwater (*Puffinus gravis*)	Burrow call	Measuring acoustic variables	High	12 m; 10 f	Brooke (1988)
	Little Shearwater (*Puffinus assimilis*)	Burrow call, flight call	Visual inspection of spectrogram	100 %	14 m; 14 f	James and Robertson (1985b)
	Manx Shearwater (*Puffinus puffinus*)	Burrow call	Visual inspection of spectrogram	High	18 m; 11 f	Brooke (1978)
	Yelkouan Shearwater (*Puffinus yelkouan*)	Burrow call	Measuring acoustic variables	100 %	28 m; 18 f (in two studies)	Bourgeois et al. (2007), Cure et al. (2009, 2011)
	Balearic Shearwater (*Puffinus mauretanicus*)	Burrow call	Measuring acoustic variables	100 %	11 m; 10 f	Cure et al. (2010)
	Cory's Shearwater (*Calonectris diomedea*)	Burrow call	Measuring acoustic variables	100 %	62 m; 45 f (in two studies)	Bretagnolle and Lequette (1990), Cure et al. (2009)
	Blue Petrel (*Halobaena caerulea*)	Burrow call	Visual inspection of spectrogram	High	404 m; 100 f	Bretagnolle (1990), Bretagnolle and Genevois (1997)
	Thin-billed Prion (*Pachyptila belcheri*)	Burrow call	Visual inspection of spectrogram	100 %	154 m; 127 f	Genevois and Bretagnolle (1995)
	Broad-billed Prion (*Pachyptila vittata*)	Burrow call	Visual inspection of spectrogram	High	Not given	Bretagnolle et al. (1990)
	Antarctic Prion (*Pachyptila desolata*)	Burrow call	Visual inspection of spectrogram	High	Not given	Bretagnolle et al. (1990)
	Fairy Prion (*Pachyptila turtur*)	Burrow call	Visual inspection of spectrogram	High	Not given	Bretagnolle et al. (1990)
	Salvin's Prion (*Pachyptila salvini*)	Burrow call	Visual inspection of spectrogram	High	Not given	Bretagnolle et al. (1990)
	Bulwer's Petrel (*Bulweria bulwerii*)	Single call, double call, repeat call	Measuring acoustic variables	No sex differences	18 m; 24 f	James and Robertson (1985c)
	Snow Petrel (*Pagodroma nivea*)	Burrow call	Measuring acoustic variables	No sex differences	26 m; 24 f	Barbraud et al. (2000)
Ciconiiformes	Oriental Stork (*Ciconia boyciana*)	Clatter	Measuring acoustic variables	100 %	7 m; 7 f	Eda-Fujiwara et al. (2004)
Charadriiformes	Black-legged Kittiwake (*Rissa tridactyla*)	Long call	Measuring acoustic variables and DFA	100 %	18 m; 14 f	Aubin et al. (2007)
	Black-legged Kittiwake (*Rissa tridactyla*)	Long call	Measuring acoustic variables and DFA	Low	41 m; 35 f	Mulard et al. (2009)
	European Herring gull (*Larus argentatus*)	Kyow alarm call, kek alarm call	Measuring acoustic variables	No sex differences	8 m; 8 f	Hardouin et al. (2013)
	Brown Skua (*Catharacta antarctica*)	Loud call, contact call, alarm call	Measuring acoustic variables and DFA	Low	20 m; 22 f	Janicke et al. (2007)
	Parakeet Auklet (*Cyclorhynchus psitacula*)	Whinny call	Measuring acoustic variables and DFA	High	8 m; 5 f	Klenova et al. (2012)
	Crested Auklet (*Aethia cristatella*)	Trumpet call	Measuring acoustic variables and DFA	No sex differences	9 m; 4 f	Klenova et al. (2012)
Strigiformes	Eastern Screech-owl (*Otus asio*)	Bounce song	Measuring acoustic variables	High	5 m; 3 f	Cavanagh and Ritchison (1987)

Table 1 continued

Order	Common and scientific names	Call type	Method	Sexing reliability	Number of birds	References
	Western Screech-owl (*Otus kennicottii*)	Bounce song	Measuring acoustic variables	100 %	15 m; 10 f	Herting and Belthoff (2001)
	Barred Owl (*Strix varia*)	One-phrased hoot, inspection call	Measuring acoustic variables	High	2 m; 4 f	Odom and Mennill (2010)
	African Wood Owl (*Strix woodfordii*)	Hoot call	Measuring acoustic variables	High	Not given	Steyn and Scott (1972)
	Eagle Owl (*Bubo bubo*)	"u-hu" call	Measuring acoustic variables	100 %	9 m; 9 f	Grava et al. (2008)
Coraciiformes	Green Woodhoopoe (*Phoeniculus purpureus*)	"kek" call	Measuring acoustic variables	100 %	41 m; 38 f	Radford (2004)
	European Bee-eater (*Merops apiaster*)	Provisioning call	Measuring acoustic variables	No sex differences	14 m; 14 f	Lessells et al. (1995)
Falconiformes	White-tailed Hawk (*Buteo albicaudatus*)	Alarm call	Measuring acoustic variables	High	3 m; 3 f	Farquahar (1993)
Psittaciformes	*Poicephalus* Parrots 6 species	Distress call	Measuring acoustic variables	Low	4–10 birds per species	Venuto et al. (2001)
	Kea (*Nestor notabilis*)	Mew call, screech call	Measuring acoustic variables	Low	Not given	Schwing et al. (2012)
Passeriformes	White-rumped Munia (*Lonchura striata phaethontoptila*)	Distant call	Visual inspection of spectrogram	100 %	13 m; 13 f	Mizuta et al. (2003)

DFA discriminate function analysis, *m* males, *f* females

not be based on behavior, appearance, nest building, incubation and parental care. Whistling ducks were named after their loud whistle calls, produced by both sexes during the year (Volodin et al. 2005a, 2009). In White-faced Whistling Ducks (*Dendrocygna viduata*), the maximum fundamental frequency of male loud whistles was always substantially lower than in females (Fig. 2). The values were non-overlapping between sexes, being <4500 Hz in males and >5300 Hz in females. After short training, sexes could be easily discriminated by ear (Volodin et al. 2003).

In Fulvous Whistling Ducks (*D. bicolor*), loud male whistles were always lower in fundamental frequency, than female calls (Fig. 3). In males, the fundamental frequency was <2100 Hz, whereas in females it was >2800 Hz. It is noteworthy that in Cuban Whistling Ducks (*D. arborea*), loud whistles by males were higher in fundamental frequency than those of females; in addition, male calls often contained a second fundamental frequency in their spectra, which resulted in biphonation (Fig. 4). In males, this fundamental frequency was >2600 Hz, whereas in females it was <2550 Hz. In loud whistles of Red-billed Whistling Ducks (*D. autumnalis*), the ranges of male and female fundamental frequency overlapped, although the duration of notes at the end part of calls was always longer in males (>0.13 s) than in females (<0.12 s) (Fig. 5). In addition, male calls contained biphonation, which was never found in female calls. In all four species of whistling ducks, the non-overlapping values of call variables provided the possibility of error free sexing by a single loud whistle (Volodin et al. 2009). As well as spontaneous vocal emission, playbacks

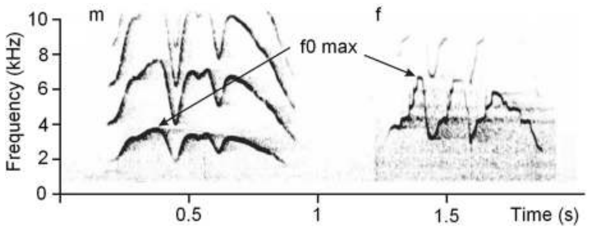

Fig. 2 Spectrogram representing loud whistle calls of (m) male and (f) female White-faced Whistling Ducks. The *arrows* point to the maximum fundamental frequency (f0max) of the calls

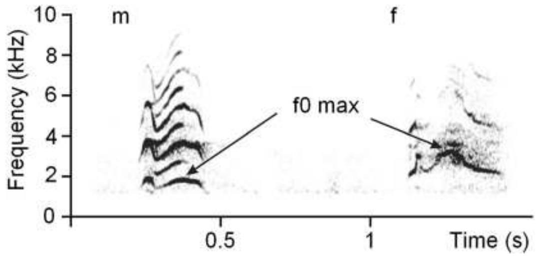

Fig. 3 Spectrogram representing loud whistle calls of (m) male and (f) female Fulvous Whistling Ducks. The *arrows* point to the maximum fundamental frequency (f0max) of the calls

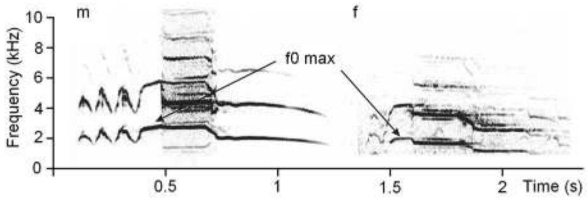

Fig. 4 Spectrogram representing loud whistle calls of (m) male and (f) female Cuban Whistling Ducks. The *arrows* point to the maximum fundamental frequency (f0max) of the calls

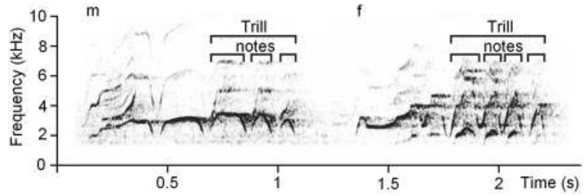

Fig. 5 Spectrogram representing loud whistle calls of (a) male and (b) female Red-billed Whistling ducks. The *brackets* point to the duration and number of notes at the end part of a call

of species-specific calls of whistling ducks evoked immediate vocal responses of loud whistles that revealed sex differences (Volodin et al. 2005b).

No sex difference was found in two-syllable calls of the Red-breasted Goose (*Branta ruficollis*) (Fig. 6). The percentage of correctly classifying calls to sex with DFA (87 %) did not differ from random values (79 %) (Volodin et al. 2008). However, in pair duets, produced during triumph-ceremony displays, the maximum fundamental frequency of female calls was always lower than in male calls; in addition, in duets, females always produced series of two-syllable calls, whereas males produced series of one-syllable calls (Fig. 6) (Volodin 1990b). The definitive triumph-ceremony (for describing the triumph-ceremony see e.g. Radesäter 1974; Volodin 1990a) is displayed only by mates of heterosexual pairs, whereas in homosexual male–male pairs only one of the males vocalizes, whereas the second male is silent (Volodin 1990c). Thus, birds of this species may be sexed by their parties in duets.

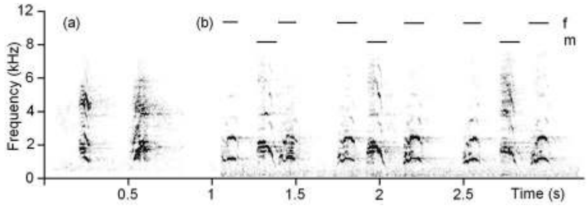

Fig. 6 Spectrogram, representing vocalizations attending the triumph-ceremony displays of the Red-breasted Geese. **a** The two-syllable call of a male and **b** a pair duet. The *horizontal lines* label (m) male and (f) female calls

In another waterfowl species, the White-fronted Goose (*Anser albifrons*), female calls during triumph-ceremony were also lower in fundamental frequency compared to male calls (Krechmar 2003). At the same time, it has been reported that in duets of the Horned Screamer (*Anhima cornuta*), vocalization is lower and harsher in the male than in the female (Gill et al. 1974). The scarcity of data precludes any general conclusions concerning the structures of male and female duet parties in Anseriformes.

Order Galliformes

The Willow Ptarmigan (*Lagopus lagopus*) represents a single monogamous species of the Tetraonidae family, where mates share parental care; the male guards the territory and the female guides the chicks (Martin and Cooke 1987). This species is practically monomorphic, males being slightly larger than females and differing slightly from females in coloration during spring. Vocal repertoire comprises 11 call types, produced by both sexes (Martin et al. 1995). Male calls are distinguished by their strong amplitude modulation, which results in wideband spectra and harsh sounds. Female calls are distinguished by their tonal structure. These differences are revealed in all call types, in particular in the "krrow" call, emitted by both sexes during territorial conflicts of pairs and during vocal interactions between parents and chicks.

Order Podicipediformes

In the Black-necked Grebe (*Podiceps nigricollis*), nesting in dense vegetation, sex dimorphism is expressed in advertising calls (Nuechterlein and Buitron 1992). Male advertising calls were lower at the start and maximum fundamental frequency and were longer compared to female advertising calls. Although the dominant frequency values did overlap between sexes, playback experiments of advertising calls to bachelor males have demonstrated that they responded to female calls and ignored male calls.

Order Columbiformes

In Orange-bellied Fruit-doves (*Ptilinopus iozonus*), male coo calls were always lower in frequency and longer than female coo calls (Baptista and Gaunt 1997). These vocal features were used for mating formation of captive pairs for conservation purposes, since this insular species has disappeared in its natural settings. As a result of breeding success, this species has been released back into the wild. In addition, the lower-frequency male calls compared to female calls have been reported for some other doves (other five species of genus *Ptilinopus*, as well as

Columba livia, *C. squamosa*, *Zenaida graysoni*, *Tutur tympanistra*, *Treron vernans*, *Phapitreron leucotis*) (Baptista and Gaunt 1997); however, measuring acoustic variables has not been conducted for these species.

In the Eurasian Collared Dove (*Streptopelia decaocto*), male coo calls were also at lower-frequency compared to female coos; however, sexing by this variable was unreliable due to slightly overlapping values between the sexes (Ballintijn and ten Cate 1997). Nevertheless, the birds could be sexed with 100 % reliability by the number of coos per sequence (from 6.3 to 11.3 in males and from 3.3 to 4.6 coos in females).

Order Caprimulgiformes

Among different calls of vocal repertoire of the Marbled Frogmouth (*Podargus ocellatus*), sex-related differences were found only in the gobble call, which both sexes produce throughout the year at territorial conflicts (Smith and Jones 1997). The gobble calls consist of low-frequency elements, repeated with intervals less than one tenth of a second. Male calls contained more elements compared to female calls (5.8 compared to 4.3 on average); their elements were shorter and were of a noticeably lower-frequency than in females, although the ranges of frequency and duration overlapped between sexes.

Order Cuculiformes

In studying the breeding system of the Pheasant Coucal (*Centropus phasianinus*), sex differences were investigated in their far-distant descending "whoops" calls and "scale" calls, produced separately or in duets (Maurer et al. 2008). Although males are lighter in weight than females (300 and 400 g, respectively), both sexes are colored similarly. Male calls were significantly higher-pitched than female calls for both studied call types. Although these authors did not provide the overall ranges of values, the average values of the dominant frequency of male calls were 1.5 times higher than in females, in both the descending whoops call (456 and 339 Hz, respectively) and in the scale call (503 and 314 Hz, respectively).

Order Gruiformes

Among Gruiformes, the possibility of reliable sexing by crowing calls has been reported for a Rallidae family species, the Purple Swamphen (*Porphyrio porphyrio*) (Clapperton 1983). The crowing call represents the territorial call, emitted by males and females at any time of day and night. Male calls are somewhat lower in fundamental frequency and purely tonal, whereas in females these calls are higher and modulated in amplitude at their end part. Due to these peculiarities in the structure, female calls sound more harsh and guttural. After training, these differences allow sexing by ear in the field (Clapperton 1983). Although males are somewhat larger than females, identifying sexes by morphometry was not possible (Craig et al. 1980).

In another Rallidae species, the American Coot (*Fulica americana*), the fundamental frequency of male calls exceeded twice that of female calls (Cosens 1981). Independently from a call type, the maximum fundamental frequency was always >1000 Hz in male calls and <1000 Hz in female calls, which allowed for identification of bird sexes by ear. In this species, external sexual dimorphism is lacking, although males, on average, are 7 % heavier than females. Probably, sex differences in calls result from differences in sizes and shape of male and female syringes (Gullion 1950), given that females are larger than males in this species.

For the Gruidae family, the problem of sexing is very important, for many cranes are endangered and require intensive captive breeding for their conservation. Sexing of the endangered Whooping Crane (*Grus americana*) is based on the maximum fundamental frequency of the guard call, exceeding 1100 Hz in females (on average, 1115 Hz) and <1000 Hz in males (on average, 946 Hz) (Carlson and Trost 1992). The value of correct classification to sex with DFA for 141 males and 118 females was 99 %, with only 3 of the 259 birds sexed incorrectly.

For White-naped Cranes (*Grus vipio*), guard calls do not allow reliable sexing (Bragina and Beme 2013). Although the fundamental frequency of female calls (on average, 1170 Hz) was noticeably higher than in male calls (on average, 790 Hz), their ranges substantially overlapped between sexes (790–1350 Hz for females and 600–1110 Hz for males, respectively) (Fig. 7). However, the sex of White-naped Cranes could be reliably identified by their duet parties, consisting of repeated syllables (Archibald 1976; Swengel 1996). Each duet syllable always started with a long male call followed with one to three short female calls (Fig. 7).

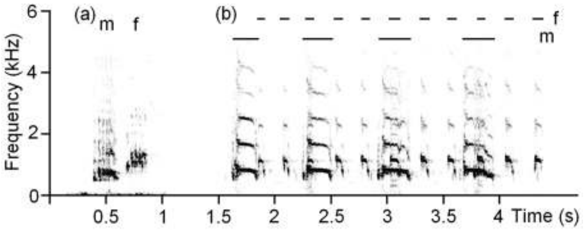

Fig. 7 Spectrogram, representing (m) male and (f) female calls of the White-naped Crane. **a** Guard call of **a** and **b** and four duet syllables. Each duet syllable consists of one long male call and of two or three short female calls

For Siberian Cranes (*Grus leucogeranus*), reliable acoustic indices of sex were not found at any call type (Bragina and Beme 2007). Although average values of fundamental frequency were higher in females in all call types, the range of frequencies substantially overlapped between sexes, precluding reliable sexual identification of any particular bird. The best discriminating ability was found in trills (Fig. 8), in which the fundamental frequency of females was not lower than 810 Hz (average 950 Hz) whereas for males, their fundamental frequency was not higher than 860 Hz (average 700 Hz). In addition, within each of nine pairs, the fundamental frequency of females was always higher than that of males. At the same time, male and female duet parties were indistinguishable, for both male and female produce one long call per each duet syllable (Fig. 8) (Swengel 1996; Bragina and Beme 2010). In duets, the average value of their maximum fundamental frequency was higher in females (1100 Hz) than in males (890 Hz); however the range of values overlapped between sexes (Bragina and Beme 2010).

In Red-crowned Cranes (*Grus japonensis*), as in other crane species, the fundamental frequency of the female in the duet call (1180 Hz) was higher on average than that of the male (1050 Hz), but bird sex could not be identified by this feature alone due to the broad overlap of their frequencies (Klenova et al. 2008). In addition, in eight of 10 breeding pairs, the fundamental frequency was always higher in female calls than in male calls, whereas in two other pairs it was always lower in females than in males. All the same, sex could be reliably assessed during duets. Duets consisted of repeated syllables, starting with a long (0.46 s) male call followed with one to four short (0.24 s) female calls (Fig. 9).

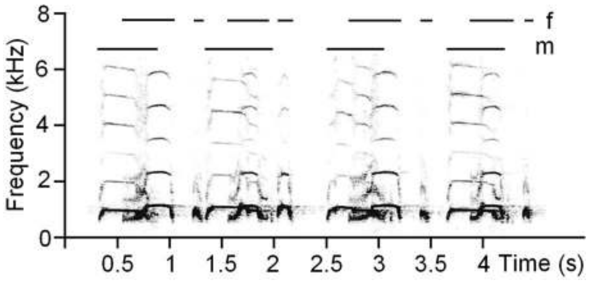

Fig. 9 Spectrogram, representing four duet syllables of a Red-crowned Crane pair. Each *syllable* consists of (m) one long male call and of (f) two female calls

Order Procellariiformes

Many species of the order Procellariiformes are nocturnal. Their calls are important for recognizing sex. Strong vocal sex differences are typical. In the Leach's Storm-petrel (*Oceanodroma leucorhoa*), sex differences were found only in one of three call types, i.e., the chatter call (Taoka et al. 1989a). Male and female chatter calls consist of syllables, differing in patterns of frequency modulation (Fig. 10). Sex-specific differences were found in the central syllables of these calls. The maximum fundamental frequency of the central syllable was always higher than 800 Hz in males (on average, 990 Hz) and lower than 750 Hz in females (on average, 650 Hz). The non-overlapping values between sexes allowed 100 % reliable sexing by voice. Birds sitting in their nesting burrows showed sex-specific responses to playbacks of chatter calls, with males selectively responding to male calls and females selectively responding to female calls.

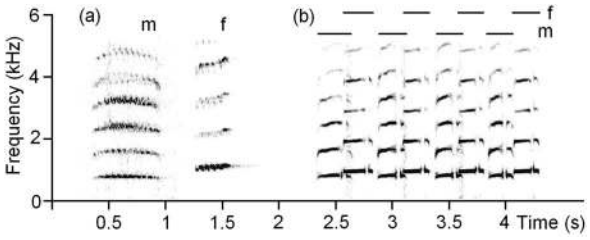

Fig. 8 Spectrogram, representing (m) male and (f) female calls of the Siberian Crane: **a** trills and **b** four duet syllables. Each *duet syllable* consists of (m) one long male call and of (f) one long female call

For Swinhoe's Storm-petrel (*Oceanodroma monorhis*), sex differences were found in the flight call, but its acoustic structure is similar to the chatter of the Leach's Storm-petrel (Taoka et al. 1989b; Taoka and Okumura 1990). Male and female calls differed by their rhythmic structure, which allowed sexes to be distinguished by ear. Birds sitting in their nesting burrows showed sex-specific responses to playbacks of chatter calls, with males selectively responding to male calls and females selectively responding to female calls.

In the Madeiran Storm-petrel (*Oceanodroma castro*), male calls were tonal and melodious whereas the female calls always contained noise and sounded harsh. The differences were sufficiently strong to allow the sexes to be distinguished by ear (James and Robertson 1985a).

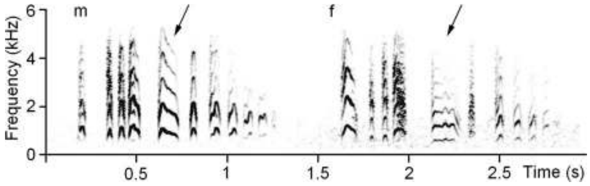

Fig. 10 Spectrogram representing chatter calls of (m) male and (f) female Leach's Storm-petrel. The *arrows* point to central sex-specific notes of the calls

In the Fork-tailed Storm-petrel (*Oceanodroma furcated*), males produce a call which is lacking in females (Simons 1981). This is a high-frequency whistle, emitted by males when they were near the entrance of a nest burrow or just in the burrow interacting with a female.

The burrow calls of the male Greater Shearwater (*Puffinus gravis*) were higher in frequency and longer compared to female calls (Brooke 1988). In the Little Shearwater (*Puffinus assimilis*) (James and Robertson 1985b), male burrow and flight calls were higher in frequency and sounded clearer compared to female calls, which were lower in frequency, more noisy and sounded gnashing. These differences allowed sexing by ear.

In the Manx Shearwater (*Puffinus puffinus*), as in previously mentioned species of Procellariformes, male calls were higher in frequency and more clearly tonal, whereas female calls were lower in frequency and noisier (Brooke 1978). The male Yelkouan Shearwater (*Puffinus yelkouan*) also vocalizes at a higher frequency than females, so that birds may be sexed with 100 % reliability using a single acoustic variable (Bourgeois et al. 2007; Cure et al. 2009, 2011). Near their nest burrows, the birds emit calls consisting of two notes, of which one is produced at inspiration and another at expiration. At inspiration, males produce a noisy note, whereas females produce a tonal note. Conversely, at expiration, males produce the tonal note, whereas females produce the noisy note. In male calls, the maximum fundamental frequency of the tonal note is always >740 Hz (on average, 885 Hz) whereas in females <530 Hz (on average, 472 Hz).

Calls of the Balearic Shearwater (*Puffinus mauretanicus*) are very similar to those of the Yelkouan Shearwater. As in the Yelkouan Shearwater, the maximum fundamental frequency of the tonal note was significantly higher in males than in females (on average, 776 and 430 Hz, respectively) and ranges of values did not overlap between sexes (Cure et al. 2010).

Calls of Cory's Shearwater (*Calonectris diomedea*) differed strongly by their shape from two previous species and consisted of four notes (Bretagnolle and Lequette 1990; Cure et al. 2009). Still, male calls again were significantly higher in fundamental frequency than calls of females. The end tonal note was the most convenient for measuring the maximum fundamental frequency: in male calls, it was always >640 Hz (on average, 739 Hz) whereas in female calls, it was always <360 Hz (on average, 291 Hz).

As well, in the Blue Petrel (*Halobaena caerulea*), male calls were higher in fundamental frequency than female calls (Bretagnolle 1990; Bretagnolle and Genevois 1997). Additionally, the rhythmic structure of calls differed strongly between sexes, since female calls included short notes that were lacking in males. A comparison of male and female calls from 11 populations confirmed the consistency of the overall pattern of male and female calls in this species.

Male and female prions: Thin-billed Prions (*Pachyptila belcheri*), Broad-billed Prions (*P. vittata*), Antarctic Prions (*P. desolata*), Fairy Prions (*P. turtur*) and Salvin's Prion (*P. salvini*), emit noisy calls from burrows, consisting of a few notes (Bretagnolle 1990; Bretagnolle et al. 1990; Genevois and Bretagnolle 1995). Sex differences were found in the temporal structure of their calls. In all five species, females always started calling with a long note, followed by short notes, whereas males started calling with a short note. These differences allowed sexing by ear.

Among Procellariiformes, there are several monomorphic species without remarkable vocal differences between the sexes. For instance, Bulwer's Petrel (*Bulweria bulwerii*) never calls during flight or while approaching a nesting colony. The vocal repertoire of this species consists of non-harmonic clicks, produced singly (single call), by two (double call) or in series (repeat call) (James and Robertson 1985c). In these calls, sex differences were poorly expressed. As a rule, females produced clicks at a higher tempo than males, but these differences were not significant.

Also, in Snow Petrels (*Pagodroma nivea*), no significant differences were found between male and female calls (Barbraud et al. 2000). Although male calls were somewhat lower in fundamental frequency, the range of values overlapped substantially between sexes. As in the Bulwer's petrel, females produced their rhythmic calls at a higher tempo than males.

Order Ciconiiformes

In the Oriental Stork (*Ciconia boyciana*), the values of dominant frequency of bill clatters (Fig. 11) were non-overlapping between sexes: they were <670 Hz in males and >703 Hz in females, that is, they were always lower in males than in females, allowing 100 % reliable sexing. In addition, the dominant frequency is negatively correlated with the bill length of the storks (Eda-Fujiwara et al. 2004).

Order Charadriiformes

In Black-legged Kittiwakes (*Rissa tridactyla*), sex differences were found in their long calls, produced by birds flying over their nests (Aubin et al. 2007). Female calls were somewhat lower in pitch compared to male calls (on average, 540 and 630 Hz, respectively) and were separated with longer intervals between three call parts. Although the values of acoustic variables did overlap between sexes, DFA allowed discrimination between

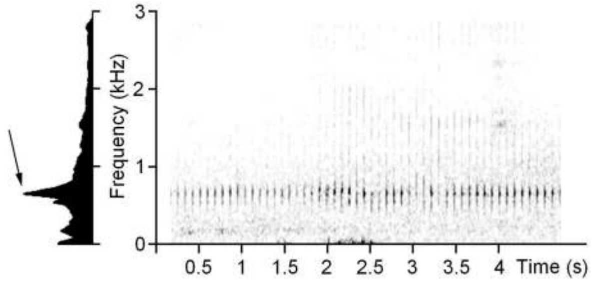

Fig. 11 Spectrogram, representing the clatter call of an Oriental Stork. The dominant frequency of the call (labeled with *arrow*) is 663 Hz, therefore the bird that produced this call was male

male and female calls with 100 % reliability. However, another study of Black-legged Kittiwakes in the same research group, conducted on another population, provided inconsistent data, with female calls being slightly higher-pitched than male calls (on average, 640 and 620 Hz, respectively) (Mulard et al. 2009). For this population, DFA showed only 69 % correct assignment of calls to sex. Consequently it remains unclear whether vocal cues to sex really exist in Black-legged Kittiwakes (Mulard et al. 2009).

No sex differences were found in the "kyow" and "kek" alarm calls of European Herring Gulls (*Larus argentatus*) (Hardouin et al. 2013). Although males are somewhat larger than females, the fundamental frequency did not differ between sexes in either call types.

No sex differences were found in the three loud call types of the Brown Skua (*Catharacta Antarctica*): loud calls, contact calls and alarm calls (Janicke et al. 2007). The value of correct assignment of calls to sex with DFA varied from only 60–73 % between call types.

For Parakeet Auklets (*Cyclorhynchus psitacula*), in which parental care of both partners is critically important for survival of the single chick, sex differences were analyzed in their self-advertising whinny calls, representing a series of trills (Fig. 12) (Klenova et al. 2012). The trills were longer in males than in females (on average, 0.39 and 0.29 s, respectively) and contained more notes per trill in males than in females (on average, 16.6 and 10.7 notes per trill). However the values did overlap between sexes and the percentage of correct assignment of calls to sex with DFA was 94 %.

However, in the closely related Crested Auklets (*Aethia cristatella*), no sex differences were found in their self-advertising trumpet calls (Fig. 13) (Klenova et al. 2012). Frequency values of all measured variables strongly overlapped between sexes. Percentage of correct assignment to sex (72 %) did not differ from random values (69 %).

Order Strigiformes

The fundamental frequency of "bounce" of the Eastern Screech-owl (*Otus asio*), emitted in response to playbacks of species-specific calls, was lower in males than in females (720 and 820 Hz, respectively) (Cavanagh and Ritchison 1987).

The bounce songs of Western Screech-owls (*Otus kennicottii*), emitted in response to playbacks of male calls, were lower in fundamental frequency in males than in females (Herting and Belthoff 2001). However the best diagnostic parameter was the dominant frequency, with non-overlapping ranges of values between sexes: always lower 725 Hz in males and always higher 725 Hz in females.

In Barred Owls (*Strix varia*), male calls were lower in fundamental frequency and longer than female calls (Odom and Mennill 2010). The maximum fundamental frequency of "inspection" calls was 590 Hz in males and 640 Hz in females, lasting 0.73 s in males and 1.20 s in females. The maximum fundamental frequency of one-phrased hoots was 540 Hz in males and 590 Hz in females, lasting 0.38 s in males and 0.76 s in females. The percentage of correct assignment of calls with cluster-analysis was 91 %.

Hoot calls by male African Wood Owls (*Strix woodfordii*) were lower in fundamental frequency compared to hoot calls of females (Steyn and Scott 1972). The 12 year long study of their population structure of this species was based on these findings (Delport et al. 2002).

Hoot calls ("u-hu" calls) of the male Eagle Owl (*Bubo bubo*) are substantially lower in fundamental frequency than hoot calls of females (Grava et al. 2008). The

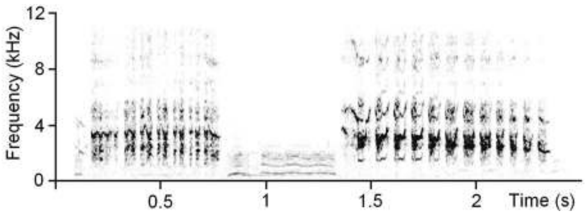

Fig. 12 Spectrogram, representing the whinny call of a male Parakeet Auklet

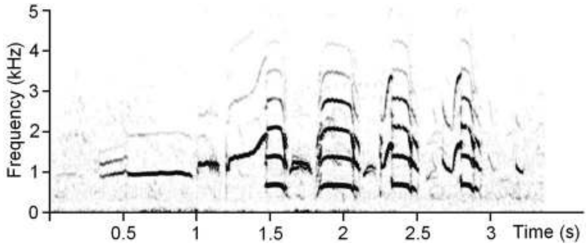

Fig. 13 Spectrogram, representing the trumpet call of a male Crested Auklet

maximum fundamental frequency of hoots was 390 Hz in males and 550 Hz in females. These differences are sufficiently strong to allow reliable discrimination between sexes by ear.

Order Coraciiformes

In the Green Woodhoopoe (*Phoeniculus purpureus*), "kek" calls were twice as low in fundamental frequency in males as in females (Radford 2004). The values of fundamental frequency did not overlap between sexes; these were lower than 600 Hz in males and higher than 700 Hz in females, which ensured 100 % reliable sexing. Although longer bills and slightly different feather coloration of males provide some indices to sex in this species, voice-based sexing is possible from a distance, which is important to a census of males and females in nature or in large enclosures.

Sex dimorphism was lacking in "provisioning" calls of the European Bee-eater (*Merops apiaster*), emitted when approaching the nest burrow (Lessells et al. 1995). In this species, males and females are of the same size, but mature males are usually a little brighter in coloration than females, noticeable when observed together (Lessells et al. 1995).

Order Falconiformes

Alarm calls of the White-tailed Hawk (*Buteo albicaudatus*) represent a rapid sequence of notes. The maximum fundamental frequency of the longest first note retains its frequency or increases it to the second note in males, but decreases in females (Farquahar 1993). This feature allows reliable discrimination between sexes. As well, this species has sex dimorphism of body size: the wings are longer and the body mass larger in females than in males.

Order Psittaciformes

For six closely related species of *Poicephalus* parrots, sex differences were investigated in their distress calls (Venuto et al. 2001). Two of the six species have external sexual dimorphism, whereas four others were sexed using laparoscopy. Distress calls of all six species represented harmonically rich, weakly modulated frequency calls, ranging between 165 and 205 Hz in fundamental frequency. Female calls were longer and higher in dominant frequency compared to male calls; however, values overlapped between sexes.

In Kea Parrots (*Nestor notabilis*), the fundamental frequency of mew and screech calls was somewhat lower in males than in females and male calls were longer than female calls (Schwing et al. 2012). However, the frequency of the variables overlapped considerably and the differences that were found were insufficient for reliable sexing.

Order Passeriformes

Among monomorphic passerines, fair sex differences have been reported for free-ranging White-rumped Munias (*Lonchura striata phaethontoptila*) from Taiwan (Mizuta et al. 2003). Distant male calls of this species contain only one note, whereas female calls contain three or more notes (on average 3.67 notes per call). This allowed 100 % reliable sexing even by ear in the field. The 100 % reliability of sexing by voice was confirmed by genetic sexing, whereas the morphometry-based sexing was only 87 % reliable.

Sexing chicks by voice

Sex differences in chick calls have been reported for discomfort calls of a few species of Galliformes. In one-day-old chicks of the Domestic Hen (*Gallus gallus*), male calls were somewhat shorter and higher in dominant frequency than in females (Tikhonov 1986). The average reliability of the acoustic sex diagnostic was 98 %, which allowed this method to be broadly applied on chick farms. Chicks of the Japanese Quail (*Coturnix japonica*), could be sexed by call duration, of 0.10–0.15 s in males and of 0.05–0.08 s in females, with 95 % reliability (Tikhonov 1986). In one-day-old chicks of the Helmeted Guinea Fowl (*Numida meleagris*), male calls were distinguished by the incidence of a frequency component (800–1300 Hz) which, when matched with the female areas of dominant frequencies (2800–3200 Hz), resulted in sexing reliability of 94–96 % (Tikhonov 1986).

In chicks of the Green Woodhoopoe "kek" calls were indistinguishable between sexes and only at the age of 3–5 months did the fundamental frequency of young males become twice as low as that of females (Radford 2004). Similarly, chick calls of American Coots were indistinguishable between sexes up to the age of 2–3 months, when female fundamental frequency decreased more than twice their original (Cosens 1981). In Cory's Shearwaters sex-specific features in calls developed only after 80 days (Bretagnolle and Thibault 1995). In chicks of the Graylag Goose (*Anser anser*), the fundamental frequency of male calls started decreasing only after 15 days; before this age chicks could not be sexed by voice (ten Thoren and Bergmann 1987).

In 59 one-day-old chicks of the Black-headed Gull (*Larus ridibundus*), male discomfort calls were lower in dominant frequency (2620 Hz), compared to females (2930 Hz); however, their range of frequencies strongly overlapped between sexes (Koshmyanova et al. 1984). In 41 male and 41 female chicks of the Barn Swallow (*Hirundo rustica*), sex differences in begging calls were completely absent at 12 day old chicks and were only very weakly expressed after 15–16 days, shortly before fledging (Saino et al. 2003, 2008). DFA conducted with a complete set of measured acoustic variables resulted in only 71 % of chicks being correctly sexed. In six males and six females the begging calls of Western Blue Bird (*Sialia mexicana*) chicks, sex differences were also lacking (Monk and Koenig 1997). Between 14 and 19 days, i.e., shortly before fledging, no one single acoustic variable showed differences between sexes. At the same time, the chicks could be sexed immediately after hatching by down coloration.

In Red-crowned, Siberian and Demoiselle (*Anthropoides virgo*) Crane chicks, no reliable acoustic sex indicators were found. With chirps from hatching to six month old chicks, the correct classification of sex with DFA was as small as 75–78 % for Red-crowned Cranes, 60–82 % for Siberian Cranes and 64–77 % for Demoiselle Cranes. In all three species, the average fundamental frequency of female calls was slightly higher than that of male calls, although the values broadly overlapped between sexes. This study was conducted with 4 male and 7 female Red-crowned Cranes, 7 male and 4 female Siberian Cranes and 8 male and 3 female Demoiselle Cranes (Goncharova et al. 2015). Sex differences were also lacking across the voice breaking in adolescent Red-crowned and Demoiselle Cranes (Klenova et al. 2010, 2014).

Conclusions: potential and limitations of bird sexing by voice

Sexing by voice is based on sex-specific calls of individual birds or on sex-specific parties in pair duets. Sexing by voice is reliable for species, in which at least one acoustic variable does not overlap in ranges of values between male and female calls, as in Collared Doves, White-rumped Munias, Oriental Storks, Green Woodhoopoes, Little Spotted Kiwi, Western Screech-owls, Eagle Owls, Leach's Storm-petrels, Yelkouan, Balearic and Cory Shearwaters, Thin-billed Prions, White-faced, Fulvous, Cuban and Red-billed Whistling Ducks, Purple Swamp Hens and American Coots.

In cases of overlapping call features between sexes, genders of particular individuals can be determined only with some degree of probability, which is usually insufficient for practical application. In these cases, voice-based sexing is considered as preliminary and used only when other methods of sexing are inapplicable. Such differences were found in the calls of Marbled Frogmouths, Black-necked Grebes, Parakeet Auklets, Kea Parrots, Barred Owls, Whooping and Siberian Cranes.

Sexing by duet is based on sex-specific call differences between males and females. This method is applicable for Red-breasted Geese, Red-crowned and White-napped Cranes. In the case of homosexual pairs, pair mates either produce the same parties (e.g. cranes), or one of the pair mates remains silent (e.g. Red-breasted Geese).

The question arises how voice-based sexing can be applied. Sometimes the differences between male and female calls are perceptually salient and can be detected by ear after short training. Sexing by ear is possible for White-rumped Munias, Little Spotted Kiwi, Eagle owls, Swinhoe's and Madeiran Storm-petrels, Manx Shearwaters, Thin-billed Prions, White-faced Whistling Ducks, Red-breasted Geese, American Coots and Red-crowned Cranes. However, in most cases for reliable sexing, it is necessary to record the call and to examine its spectrogram. This can be done with inexpensive recorders and spectrographic software, freely available from the internet (e.g. see http://www.syrinxpc.com; http://auditoryneuroscience.com/acoustics/spectrogram_software; http://sourceforge.net/projects/arss/; http://www.fon.hum.uva.nl/praat/).

However, the main requirement for successful voice-based sexing is the collection of a sufficient number of acoustic recordings for analysis. In some cases, vocal responses from subject birds can be provoked by playbacks of species-specific calls, available from sound libraries, such as that at http://www.bioacoustica.org/, or even in response to their simulation by researchers (e.g. for Black-necked Grebes, Western Screech-owls, Leach's and Swinhoe's Storm-petrels, Whistling Ducks). The playback approach is especially useful when only a few or even a single bird of the required species is kept in an enclosure, as is common in zoos. Otherwise, recordings can be time-consuming, the main limitation for employing voice-based sexing for monomorphic birds. All the same, playbacks should be applied carefully, after consulting with experienced specialists on the biology of a given species. For instance, playbacks can destroy the structure of humming-bird leks, for these birds are intolerant to the presence and voices of alien conspecifics at some stages of their reproductive cycle (Baptista and Gaunt 1997).

For researching sex-related call features in previously unstudied monomorphic species, it is necessary to include many (20 and more) individually marked birds of known sex (birds can be sexed e.g., genetically or by postmortem). It is also necessary to have regular access to birds in different situations for recording different call types and, by agreement with and the assistance of keepers, use procedures to stimulate vocal activity, e.g. the temporary separation of birds with wire mesh. A very interesting and poorly studied aspect of such research is the ontogenetic period of establishing the sex differences of vocalization. Consequently, in working with chicks, it is necessary to conduct regular recordings at different stages along maturation.

Vocal sex dimorphism is expected to be found to a high degree in completely monomorphic birds and/or when visual identification of sex by conspecifics is complicated for some reason (e.g. Klenova et al. 2012). These are nocturnal species (e.g. owls, goatsuckers, Procellariformes), species inhabiting dense vegetation (ratites, parrots, Passeriformes), or nesting in burrows (Procellariformes, Charadriiformes, penguins). Also, prominent differences between male and female calls are expected to be found in species with prominent sexual dimorphism of their vocal anatomy (e.g. some waterfowl). In addition, there is a higher possibility of finding remarkable sex differences in calls, when these differences were already found in a related species. Consequently, voice-based sexing may be used either as a feasible alternative to classical invasive techniques of sexing or for verifying their results, both in captivity and in the wild.

Abbreviations

DFA: discriminate function analysis; Hz: hertz; f0: the fundamental frequency; f0max: the maximum fundamental frequency; f0start: the fundamental frequency at the beginning of the call; fpeak: the dominant frequency, i.e., the maximum amplitude frequency of a call, where maximum energy is concentrated; duration: the call duration; interval: the inter-call interval.

Authors' contributions

All authors collected and systematized literature for the review. IV and EV prepared the earlier draft of the manuscript. All authors equally participated in editing the manuscript. All authors read and approved the final manuscript.

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Acknowledgements

The authors are sincerely grateful to the anonymous reviewers for their valuable comments provided to the manuscript. This study was supported by the Russian Foundation for Basic Research (grants 12-04-00260a to IV, EV and VM and 12-04-00414a to AK, for studying the acoustic-based, laparoscopy and gene-based methods of sexing of a few Anseriformes, Gruidae and Alcidae species included in this review), by the President RF Foundation (Grant MK-1781.2012.4 to AK, for studying Alcidae species, also included in this review) and by the Russian Scientific Foundation (Grant No 14-14-00237) to IV, EV, AK and VM for completing the review.

Competing interests

The authors declare that they have no competing interests.

Received: 22 October 2014 Accepted: 3 November 2015

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