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SEX DIFFERENCES IN THE VOCALIZATIONS AND SYRINX OF THE COLLARED DOVE (*STREPTOPELIA DECAOCTO*)

MECHTELD R. BALLINTIJN[1] AND CAREL TEN CATE

Section of Ethology, Institute of Evolutionary and Ecological Sciences, Leiden University, P. O. Box 9516, 2300 RA Leiden, The Netherlands

ABSTRACT.—We examined differences between sexes in the structure of vocalizations and the syrinx of the Collared Dove (*Streptopelia decaocto*). Seven vocal characteristics were measured to determine the degree of sex differences in the structure of the "perch-coo." Sex differences in vocalizations occurred in vocal activity levels and spectrotemporal parameters. Females produced fewer and shorter coo bouts. Coos produced by females also had a higher fundamental frequency, more overtones, a different temporal pattern, and tended to be less stereotyped. Discriminant function analysis revealed that sound percentage, followed by modulation percentage and fundamental frequency, were best at discriminating between the sexes. Based on the magnitude of sex differences and acoustic discrimination ratios, the latter two characters are the ones most likely to be used for vocal sex recognition. In general, the syrinx of female Collared Doves is a reduced copy of the one found in males. Trachea size and the number of tracheal and bronchial rings had high loadings on the principal components that showed significant differences between the sexes. In addition to general size differences, the number of ventromedially thickened rings and length of the tracheosyringeal membrane also were strongly correlated with these principal components. Length and height of the primary bronchi did not appear to differ between the sexes but were bilaterally asymmetrical only in males. The combination of vocal and anatomical data provides evidence that morphological aspects contribute to sexual dimorphism in vocalizations. *Received 26 February 1996, accepted 26 July 1996.*

SINGING WAS LONG THOUGHT to be a male behavioral trait, whereas female song was viewed as rare and exceptional (Nice 1943). Nowadays, singing is recognized as a regular feature of female behavior with a distinct biological function (Ritchison 1983, Arcese et al. 1988, Baptista et al. 1993). Despite recent interest in female song, little is known about its acoustical structure. This might be due to the fact that male and female songs often are so different that they share few spectrotemporal characteristics.

Studies of female song vary from describing song types and categories (e.g. Seutin 1987, Arcese et al. 1988, Brown and Farabaugh 1991) to systematically measuring the spectrotemporal structure of female song (Beletsky 1982, 1983) and comparing it with the structure of songs produced by males (Gahr and Güttinger 1986, Hoelzel 1986, Baptista et al. 1993). In addition, extensive analyses of sexual differences in calls are available for several species of passerines (Zann 1984, Okanoya and Kimura 1993) and nonpasserines (Exo 1984; James and Robertson 1985a, 1989; Cavanagh and Ritchison 1987; Dooling et al. 1987; Rosenfield and Bielefeldt 1991; Robisson 1992; Farquhar 1993).

Sex differences may be present in vocal activity, frequency characteristics, temporal patterning, and syntax of the vocalization, but few studies have examined all of these parameters within the same species. Furthermore, the nature of differences between males and females is not unidirectional for all species. Nonetheless, the mere presence of sex differences in the structure of calls and songs leads to the question of how vocal differences between males and females arise.

Differences in the structure of the syrinx have been proposed to explain sex differences in the fundamental frequency of vocalizations. In most of the species studied, the larger sex produces the lowest frequency (e.g. James and Robertson 1989, Rosenfield and Bielefeldt 1991, Farquhar 1993). A larger body size usually is interpreted as a larger syringeal apparatus, which in turn produces lower frequencies (between species: Ryan and Brenowitz 1985; within species: Würdinger 1970). Yet, females of several owl species are larger than males but have smaller syringes and higher-pitched vocalizations (Miller 1934), indicating that body size does not always reflect

[1] E-mail: ballintijn@rulsfb.leidenuniv.nl

syrinx size. Because sex differences in vocal parameters can not always be explained by sexual dimorphism in body size, knowledge of the syringeal anatomy of both sexes is necessary to gain insight into the causation of sex differences in vocalizations.

Theoretically, sex differences in vocalizations may arise because: (1) males and females have a similar syrinx, but make different use of the vocal apparatus; (2) differences in anatomy are present, but males and females use their syrinx in the same way; or (3) males and females differ both in syrinx structure and in the way sound is produced (e.g. Mallards [*Anas platyrhynchos*]; Lockner and Youngren 1976). Detailed information on sex differences in both vocalization structure and syringeal anatomy must be combined with models concerning sound production to distinguish among these possibilities (e.g. Brackenbury 1982, Gaunt and Gaunt 1985, Nowicki and Marler 1988). Furthermore, combining information on syringeal and vocal sex differences may shed light on the role specific syringeal structures play in determining the acoustical structure of vocalizations. For some morphological structures it is known which acoustical parameter is influenced by the structure (e.g. medial tympaniform membranes determine the fundamental frequency of a sound [Würdinger 1970, Abs 1980]). For other aspects of vocal structure, such as the production of overtones, it is less clear which syringeal structure is responsible (Nowicki and Marler 1988). By comparing syringes that share the same basic structure, like the male and female syrinx, but produce vocalizations with a distinctly different structure, insight can be gained into how syringeal structures influence specific aspects of a vocalization. However, few studies have described sexual differences in anatomy of the syrinx (Myers 1917; Appel 1929; Warner 1971, 1972), and even fewer have compared sex differences in syringeal anatomy with those in the structure of vocalizations (Miller 1934, Platz 1974, Lockner and Youngren 1976).

The Collared Dove (*Streptopelia decaocto*) is a nonpasserine with a relatively simple and stereotyped vocalization, the "coo" (Gürtler 1973, ten Cate 1992). The vocal characteristics and syringeal anatomy of this species make it an excellent subject for examining vocal and anatomical sex differences in the sound-producing system (see Ballintijn et al. 1995). As in many dove species, Collared Doves produce three coo types (Goodwin 1954, Cramp 1985, ten Cate 1992). The "bow-coo," functioning in both territorial defense and courtship, is produced only by males, whereas the "perch-coo," given in the context of territorial defense, and the "nest-coo," given during nesting activities, are produced by both sexes (Cramp 1985). In the Collared Dove, all coo types have the same basic structure (Gürtler 1973, ten Cate 1992). Male and female perch-coos and nest-coos share this structure, but sexual differences are assumed to be present. Compared with males, females produce fewer (Hofstetter 1954) and softer vocalizations (Nowak 1965) that also are higher-pitched (Ferianc 1947 *in* Cramp 1985). However, these differences have not been quantified. The aim of our study was to: (1) assess the presence of sexual differences in the structure of vocalizations by measuring a large set of vocal parameters, including frequency characteristics, temporal patterning, and overall vocal activity; and (2) investigate sexual differences in the anatomy of the syrinx. Analyses combining both vocal and syringeal sex differences may provide insight into the causation of sexual dimorphism in vocalizations and the role of specific syringeal structures in determining the acoustical structure of vocalizations.

Methods

Study animals and housing.—Nine male and six female Collared Doves were used to study sexual differences in characteristics of the perch-coo. Individuals were divided into two groups according to year of birth. Individuals of group I (four males, four females) were born in 1992, and individuals of group II (five males, two females) were born in 1993. Both groups were kept with their parents in outside aviaries after hatching; at the age of 5–6 weeks all individuals were isolated from adults. Individuals in group I were visually isolated from each other, but could interact vocally. A year later individuals in group II were placed with group I in the same room. Individuals in group I could hear only individuals of their same age during the first year, whereas those in group II also were exposed to vocalizations of birds in group I, which were one year older. The wooden cages measured 70 × 60 × 60 cm and had a wire mesh front. Food (a commercial seed mixture) and water were available *ad libitum*. Individuals were maintained on a 13L : 11D photoperiod (light onset at 0800) at a temperature of 21°C.

Recordings.—Vocalizations were recorded for Group I and II individuals in 1994 and 1995, respectively. Weekly video recordings were conducted when birds

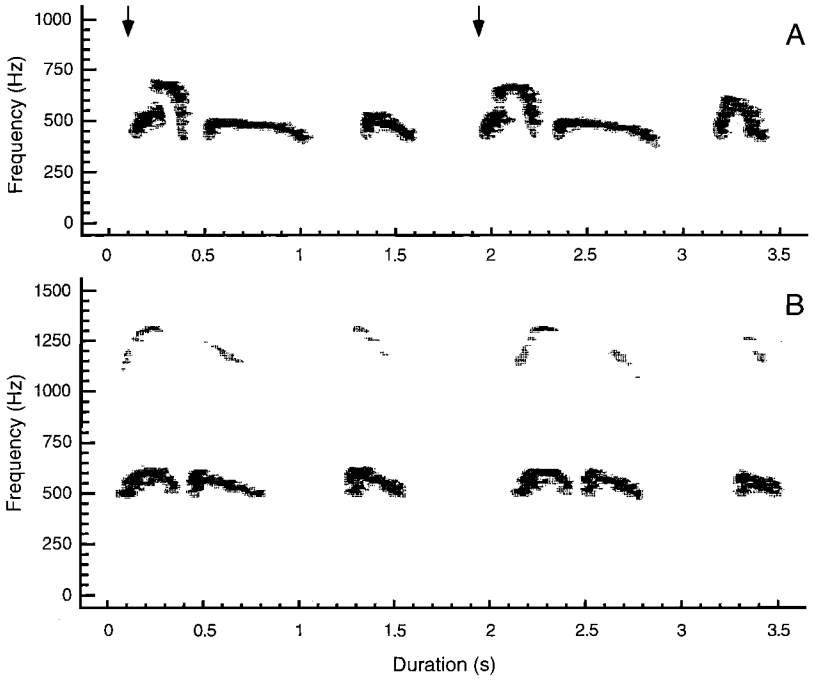

Fig. 1. Sonograms of two perch-coos of a male (A) and female (B) Collared Dove. Arrows indicate the beginning of coos. Note the characteristic differences between male and female cooing: the presence of modulations (the first element of the first male coo, and first and third elements of the second male coo are modulated) and a lower fundamental frequency for unmodulated elements in males, and the presence of one overtone in females.

were between 68 and 84 weeks old. Cooing was recorded on video (Sony U-matic VO-5800PS) using a tape recorder (Sony TC-D5) as an amplifier to support an external microphone (Sennheiser MKH 50). Care was taken to avoid systematic differences in recording distances and levels. After each session, the coo bouts were transferred from videotape to audiotape. Recordings began between 0800 and 0830 and lasted for 2 h. Because females produced very few coo bouts, additional recordings were made to obtain enough data for statistical analysis. The additional recordings were made with a similar setup but were of variable duration and did not include all individuals.

Body measurements and sex determination.—Body mass (± 2 g), tarsus length (± 0.1 mm), bill length (± 0.1 mm), and head length (± 0.1 mm) were measured for each bird at the age of ca. 84 weeks. Sex determination was based on breeding behavior (including egg-laying; two males, one female), dissection (three males, three females), and the presence of bow-cooing (four males). In the closely related Ringed Turtle-Dove (*S. risoria*), bow-cooing is a behavioral trait specific to adult males (Nottebohm and Nottebohm 1971, Cheng and Lehrman 1975). Furthermore, it was never seen in adult female Collared Doves during the many years of research at our laboratory (pers. obs.). A discriminant function analysis (see below) with four body measures (body mass, tarsus length, bill length, and head length) as independent variables, and based on 31 males and 12 females housed at the laboratory, was used to sex two females that could not be sexed using the above criteria. The discriminant scores used to sex these two individuals assigned the correct sex to 29 of the 31 males (93.5%) and 10 of the 12 females (83.3%).

Analysis of coo structure.—Our analyses focused on the perch-coo, which is the most prevalent coo-type emitted by male and female Collared Doves in the laboratory. A coo consists of three elements (Figs. 1 and 2), which can be considered separate units of production (ten Cate and Ballintijn 1996). Each element of a coo can occur in two variants. Unmodulated elements have a relatively constant (or slight bow-shaped) frequency during the whole element, and modulated elements are characterized by a discrete upward shift at the beginning and a downsweep at the end (Fig. 1A; Gürtler 1973, ten Cate 1992). The coos are given in series, called "coo bouts."

Seven vocal parameters of the perch-coo were analyzed. To determine the overall vocal activity of an individual, we measured the average number of coo bouts produced in a 2-h period. For this parameter only the weekly recordings were used. All bouts produced by an individual, during both the weekly and additional recordings, were used to calculate the av-

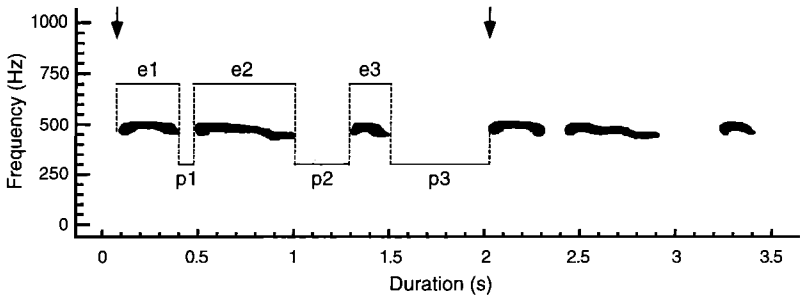

Fig. 2. Schematic representation of two coos, indicating temporal characteristics measured. Arrows indicate the beginning of coos. A coo consists of three elements (e1, e2, and e3), two pauses within a coo (p1 and p2), and one pause between coos (p3).

erage bout length (expressed as the number of coos given in one series). The same set of coo bouts was used to determine the modulation percentage (i.e. the percentage of elements that occurs in the modulated form). For statistical analysis of the other vocal parameters (i.e. frequency profile, harmonic structure, stereotypy, and temporal structure), a set 15 coos per individual was selected. However, because some individuals (especially females) produced only a few coo bouts, set size varied from 3 to 15 coos. To minimize intraindividual variation in the vocal parameters, each of the selected coos had to be: (1) unmodulated for all three elements, and (2) the first coo of a bout. Using the SIGNAL sound analysis system (Engineering Design), each coo was digitized (sample rate of 12,500 Hz; 16-bit precision) and stored in a computer file. To obtain the frequency profile of a coo, power spectra (based on 256-point transforms and excluding energy below 300 Hz and above 800 Hz; frequency resolution 6 Hz) were generated for all three elements of the coo. The fundamental frequency of an element was determined by measuring the frequency at peak amplitude.

The coo of the Collared Dove is an almost pure tone (Gürtler 1973), with most of the acoustic energy concentrated at the fundamental frequency. Nevertheless, overtones may be present. To calculate the number of overtones, we generated a power spectrum for the second element of the selected coos and determined the fundamental frequency. Because overtones are multiples of the fundamental frequency, the amplitude (and frequency) of an overtone was determined by measuring peak amplitude in a section of the power spectrum where an overtone was expected (section = $n \times$ fundamental frequency $\pm$ 50 Hz, for n = 2 to 6). The harmonic structure was defined as the number of overtones having an absolute amplitude of more than -70 dB.

The stereotypy of cooing was measured by calculating digital spectrogram cross-correlations (Clarke et al. 1987) within each individual (Nelson et al. 1995); spectrograms from 3 to 15 coos were generated. Spectrograms were cross-correlated with each other (resulting in 6 to 210 cross-correlations), and the mean correlation coefficient was calculated. The closer the mean correlation coefficient is to one, the more stereotyped the coo structure of an individual.

The temporal structure of coos was analyzed using real time spectrograms produced by SIGNAL (sample rate of 12,500 Hz; time resolution of 7 msec). The duration of the elements and pauses of a coo (Fig. 2) were measured using an on-screen cursor.

Morphology of the syrinx.—Structures of the trachea, syrinx, and bronchi were measured to assess differences between sexes in the sound-producing system. Six male and nine female Collared Doves (two years of age, lab-reared) were overdosed with Nembutal (300 mg/kg body mass, intramuscular.) before perfusing with 250 ml saline, followed by 300 ml 4% formaldehyde in distilled water. After perfusion-fixation, the trachea and bronchi were removed by block dissection. Next, we used a Nikon profile projector V-16A with a magnification of 10 × and an accuracy of 0.1 mm to measure: length and diameter of the trachea; insertion of the Mm. sternotracheales; length, height, and width of the primary bronchi; and height and depth of the lateral tympaniform membranes.

The syringes of 14 males and 10 females (age unknown, dying from natural causes or hunting) were block-stained with a combined cartilage-bone stain (Alcian Blue-Alizarin Red). Using a Zeiss stereoscopic microscope (magnification 60–250 ×) the following measures were taken: number of rings in trachea and bronchi, degree of ossification, number of cartilage connections between rings, and length and position of maximal width of the tracheosyringeal membrane.

The syringes of four males and eight females measured directly after perfusion-fixation were further processed for light microscopical study. Following perfusion-fixation and dissection, syringes were decalcified (Bouin-fixative or 10% formic acid), dehydrated, and stored in alcohol. After embedding in paraffin, 7-μm horizontal sections were cut with a rotary microtome in such a plane that trachea and bronchi were visible in one section. Sections were mounted on slides and stained (Weigert-Van Gieson).

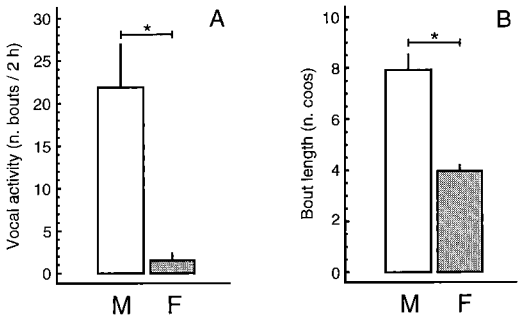

Fig. 3. Sex differences in (A) vocal activity (number of coo bouts produced during a 2-h period), and (B) bout length (number of coos given in one series). Values are mean and standard error. Asterisks indicate significant difference between sexes after Bonferroni correction.

Length of the elastin band and position of the related transition in tracheal epithelium (Ballintijn et al. 1995) were determined using a Nikon Labophot-2 compound microscope (magnification 40–400 ×).

Statistical analyses.—Outliers were identified with a discordancy test for univariate samples (Barnett and Lewis 1994), and data were tested for normality (one-sample Kolmogorov-Smirnov test). Except for modulation percentage, all parameters (vocal and morphological) were normally distributed. To investigate the effects of sex on normally distributed vocal parameters a two-way ANOVA was conducted with sex and group (year of birth) as independent variables. The interaction factor between sex and group was never significant and was omitted from the analysis. A Mann-Whitney-*U* test was used to analyze sex differences in modulation percentage, and a sequential Bonferroni technique was used to correct for multiple testing (Rice 1989).

Measurements of the syrinx were divided in three groups: (1) those directly taken after perfusion-fixation, (2) those taken from cartilage-bone stained syringes, and (3) those taken from horizontal sections. We used principal components analysis (PCA) to reduce the number of variables in the first two groups of syrinx measurements. Four principal components with eigenvalues >1 were extracted for each set of data. To test for differences between sexes, the regression scores of each of these components were used as dependent variables in a one-way ANOVA. Measurements from horizontal sections (i.e. the third group) were tested directly in a one-way ANOVA with sex as the independent variable (Bonferroni tests were used to correct for multiple testing). Two stepwise discriminant function analyses (DFA) were conducted to evaluate which vocal parameters best discriminated between the sexes (Wilks λ; minimum F to enter = 2.0, maximum F to remove = 1.5). The first DFA included all seven vocal parameters (vocal activity, bout length, modulation percentage, fundamental frequency, harmonic structure, stereotypy, and temporal pattern), and the second DFA included only the five spectrotemporal parameters (modulation percentage, fundamental frequency, harmonic structure, stereotypy, and temporal pattern). Except for the outlier analysis, all analyses were performed using SPSS/PC+, and all tests were two-tailed.

RESULTS

Sex differences in the perch-coo.—On average, males produced 15 times as many coo bouts as did females ($F = 9.98$, df = 1 and 12, $P = 0.008$; Fig. 3A). Some males produced 90 bouts in 2 h, or one coo bout every 80 s. In contrast, no female produced more than seven bouts in a 2-h period. Males also produced significantly more coos per bout than did females, averaging 6.3 to 11.3 versus 3.3 to 4.6 in females ($F = 32.39$, df = 1 and 12, $P < 0.0005$; Fig. 3B).

The production of modulations was mostly confined to males (Figs. 1A and 1B). Only one of nine males did not produce modulated elements; all others had modulation percentages varying from 5 to 97% (≥50% in six males). In contrast, only one female produced modulations, and her modulation percentage was only 5%. The difference in modulation percentage between males and females was highly significant ($Z = -2.7386$, $P = 0.005$; Fig. 4A).

The fundamental frequencies of all three elements were averaged to calculate the fundamental frequency of a coo. Males produced significantly lower fundamental frequencies than did females ($F = 9.23$, df = 1 and 12, $P = 0.01$; Figs. 1 and 4B). On the level of the individual, the frequencies produced by males and females overlapped considerably. Individual means varied from 495–606 Hz in males and from 563–736 Hz in females. Male coos had half as many overtones as coos produced by females ($F = 7.84$, df = 1 and 12, $P = 0.016$; Fig. 4C), but the range of individual means among males (1.3–2.8 overtones) was completely encompassed by the range among females (1.0–5.6 overtones).

Spectrogram cross-correlations revealed a strong tendency for male cooing to be more stereotyped than female cooing ($F = 4.46$, df = 1 and 12, $P = 0.056$; Fig. 5A). In males, individual means varied from 0.74 to 0.89, and eight of nine males had correlation coefficients >0.78. Variation among females ranged from 0.69 to 0.84, but only two of six females had correlation coefficients >0.78.

Measurements of the temporal structure of

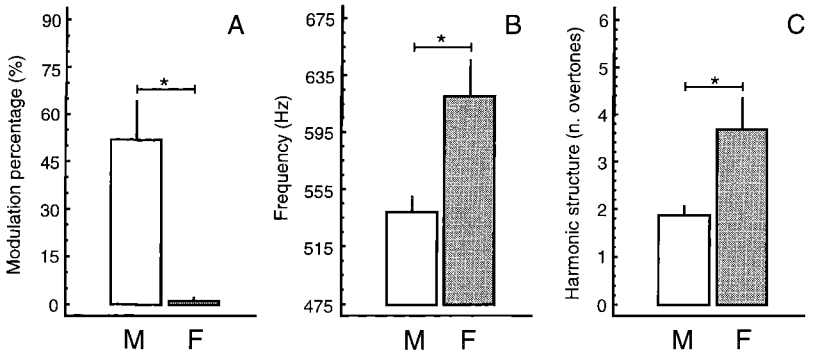

Fig. 4. Sex differences in (A) modulation percentage, (B) the fundamental frequency of the coo (averaged over the three elements), and (C) the harmonic structure (i.e. the number of overtones with an amplitude greater than −70 dB). Values are mean and standard error. Asterisks indicate significant difference between sexes after Bonferroni correction.

the coos were used to calculate the proportion of actual sound in a coo (i.e. the duration of the three elements/total duration of the coo). In males, the elements made up >55% of coo duration, whereas in females this value was just above 45% ($F = 17.26$, df = 1 and 12, $P = 0.001$; Fig. 5B). Thus, males had a higher vocal output per coo than did females.

In the first stepwise DFA, which included all vocal parameters, bout length was entered first ($P = 0.001$) and explained 71.6% of the variation between males and females. In the following steps modulation percentage ($P < 0.0005$) and fundamental frequency of the coo ($P < 0.0005$) were included, increasing the explained variation to 84.2% and 88.7%, respectively. None of the other vocal parameters was incorporated in the discriminant function. Bout length alone was sufficient to correctly classify all males and females.

The second stepwise DFA was based on spectrotemporal characteristics of the coo only. The parameters entered the DFA in the following order: percentage of sound in the coo ($P = 0.001$), modulation percentage ($P = 0.001$), frequency of the coo ($P < 0.0005$), harmonic structure ($P < 0.0005$), and stereotypy ($P < 0.0005$). The percentage of variation explained by the discriminant function increased from 56.5% (including only sound percentage) to 90.1% (including all five spectrotemporal parameters). The discriminant function based on the percentage of sound alone correctly identified all males and five of the six females (83.3%). The latter value increased to 100% when modulation percentage, frequency, and harmonic structure were included in the discriminant function.

Sex differences in syrinx morphology.—The results of the principal components analysis for syrinx measures taken directly after perfusion-fixation are summarized in Table 1. The first principal component (PC1a) accounted for 28.9% of the variance in the data, and the second (PC2a), third (PC3a), and fourth (PC4a) components explained an additional 21.5%, 17.0%, and 10.5% of the variance, respectively. Measures of the trachea loaded highly on PC1a, whereas PC2a showed high correlations with lateral tympaniform membrane measures. In contrast, PC3a and PC4a did not seem to represent a clear morphological structure, although PC3a mostly related to measures of the primary bronchi. Only PC1a showed a significant effect of sex ($F = 34.14$, df = 1 and 12, $P < 0.0005$).

The second PCA concerned measures of the cartilage-bone stained syringes (Table 2). The

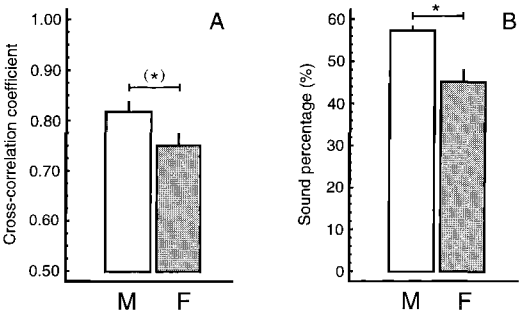

Fig. 5. Sex differences in (A) stereotypy of cooing (cross-correlation coefficient), and (B) sound percentage of a coo. Values are mean and standard error. Asterisks indicate significant difference between sexes after Bonferroni correction.

TABLE 1. Factor loadings of each syrinx measure (taken after perfusion-fixation) on the first (PC1a), second (PC2a), third (PC3a), and fourth (PC4a) principal component. Also given are eigenvalues, the cumulative variance explained by the components, and the main morphological structure represented by each component. T1, first tracheal ring; LTM, Lateral Tympaniform Membrane; ST, Mm. Sternotracheales.

Syrinx measures	PC1a	PC2a	PC3a	PC4a
T1-glottis	0.815	0.104	−0.100	−0.339
T1-insertion ST	0.585	−0.318	−0.106	−0.566
Insertion ST	0.787	−0.042	0.439	−0.107
Longest diameter	0.745	−0.234	−0.207	0.261
Shortest diameter	0.592	−0.241	−0.571	0.291
Bronchial length (l)[a]	0.321	−0.540	0.521	0.224
Bronchial length (r)[b]	0.232	−0.229	0.742	0.570
Bronchial width	0.449	−0.486	−0.107	0.005
Bronchial height (l)	−0.262	−0.066	0.801	−0.414
Bronchial height (r)	0.820	0.096	−0.081	−0.046
LTM height (l)	0.416	0.689	0.468	0.270
LTM height (r)	0.417	0.448	0.288	−0.458
LTM depth (l)	0.201	0.808	−0.077	0.179
LTM depth (r)	0.177	0.924	−0.130	0.085
Eigenvalue	4.049	3.002	2.239	1.469
Cum. variance	28.9%	50.4%	67.4%	77.9%
Morphological structure	trachea	LTMs	bronchi	—

[a] Left side of syrinx.
[b] Right side of syrinx.

four principal components explained 33.6%, 18.6%, 14.8%, and 13.0% of the variance, respectively. Most syrinx measures loaded highly on the first principal component (PC1b). PC2b and PC3b each were represented by a single measure: maximum width of the tracheosyringeal membrane for the second component and number of bronchial rings containing bone for the third component. PC4b did not appear to represent a specific morphological structure. Significant differences occurred between males and females for PC1b ($F = 9.11$, df = 1 and 18, $P = 0.008$), but the other principal components did not differ significantly between the sexes.

On average, the male trachea was constructed of 108 rings and had a length of 77 mm, and the female trachea contained fewer than 102 rings and had a mean length of 71 mm (Fig. 6, Tables 3 and 4). Trachea length was highly correlated with both PC1a (actual length; Table 1) and PC1b (number of rings; Table 2). Both of these principal components were significantly affected by sex. Because Collared Dove tracheas are slightly oval-shaped, two diameters were

TABLE 2. Factor loadings of the different measures taken from cartilage-bone stained syringes on the first (PC1b), second (PC2b), third (PC3b), and fourth (PC4b) principal component. Also given are eigenvalues, the cumulative variance explained by the components, and the main morphological structure represented by each component. TSM, tracheosyringeal membrane.

Syrinx measures	PC1b	PC2b	PC3b	PC4b
No. of tracheal rings	0.583	0.425	−0.188	0.480
No. of bronchial rings (l)[a]	0.776	−0.504	−0.126	0.092
No. of bronchial rings (r)[b]	0.753	−0.514	−0.101	0.102
Ventromed. thickened rings	0.570	0.341	0.145	−0.514
No. of connecting sheets	0.506	0.266	0.456	0.505
Length TSM	0.637	−0.025	0.472	−0.467
Max. width TSM	0.235	0.772	−0.148	−0.072
Bronchial rings with bone	−0.368	−0.099	0.806	0.206
Eigenvalues	2.687	1.492	1.185	1.033
Cum. variance	33.6%	52.2%	67.0%	80.0%
Morphological structure	syrinx size	width TSM	ossification	—

[a] Left side of syrinx.
[b] Right side of syrinx.

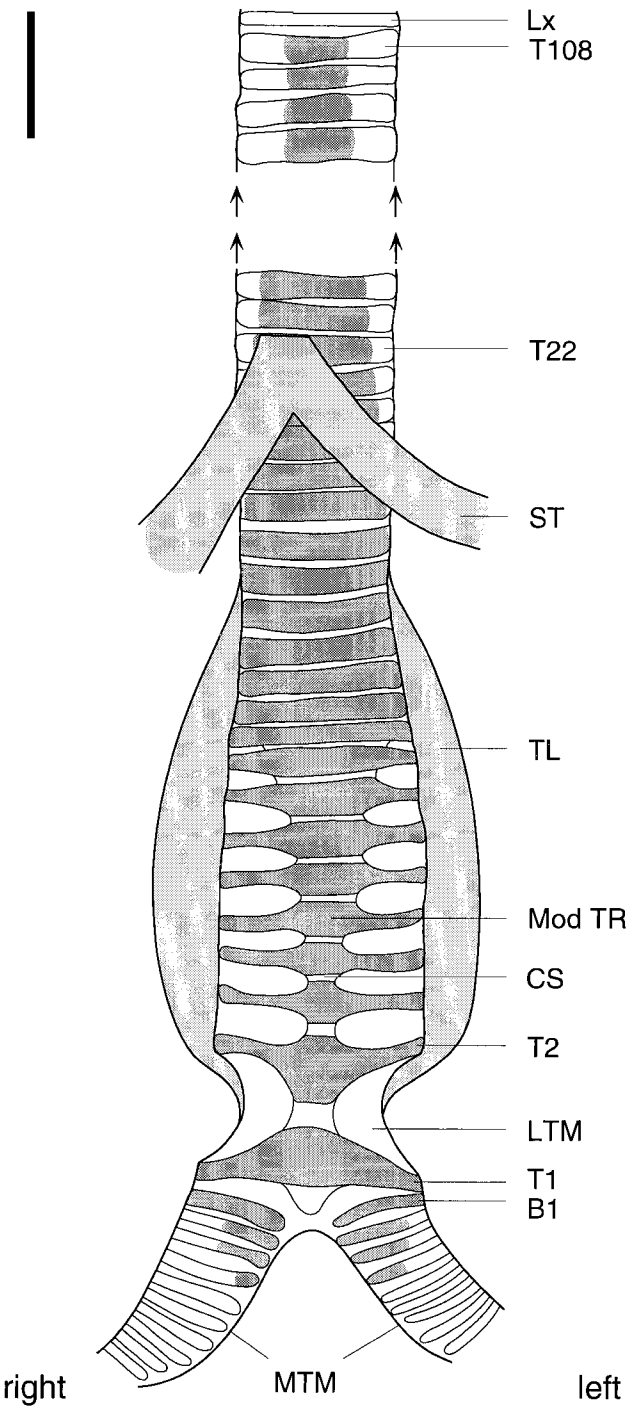

Fig. 6. Ventral view of the Collared Dove syrinx. MTM, medial tympaniform membranes; LTM, lateral tympaniform membranes; ST, Mm. sternotracheales; TL, Mm. tracheolaterales; Mod TR, modified tracheal rings (thickened over the ventral midline); CS, cartilage sheet; T1, first tracheal ring; T2, second tracheal ring; B1, first bronchial ring; Lx, larynx. Dark gray structures are ossified tissue; light gray structures are muscle tissue; white structures are cartilaginous or membranous tissue. Scale bar = 2 mm.

TABLE 3. Sexual differences in syringeal measures taken directly after perfusion-fixation. T1, first tracheal ring; LTM, Lateral Tympaniform Membrane; ST, Mm. Sternotracheales (except for volume in mm³, and muscle insertion in number of tracheal rings, measures are given in mm).

Syrinx measures	Males $\bar{x}$ SD	*n*	Females $\bar{x}$ SD	*n*
Tracheal measures				
T1-glottis	77.0 ± 7.7	6	70.6 ± 3.7	9
T1-insertion ST	16.7 ± 0.06	5	15.1 ± 0.24	9
Insertion ST	23.0 ± 1.1	6	20.2 ± 1.6	9
Longest diameter	4.0 ± 0.04	6	3.7 ± 0.03	9
Shortest diameter	3.3 ± 0.04	6	2.7 ± 0.27	9
Diameter long/short	1.21 ± 0.15	6	1.37 ± 0.16	9
Bronchial measures				
Bronchial length (l)[a]	4.30 ± 0.78	5	4.18 ± 0.62	9
Bronchial length (r)[b]	5.11 ± 0.6	5	4.68 ± 1.05	9
Bronchial height (l)	1.64 ± 0.14	5	1.87 ± 0.35	9
Bronchial length (r)	2.08 ± 0.31	5	1.85 ± 0.22	9
Bronchial width	3.15 ± 0.20	6	3.11 ± 0.14	9
LTM measures				
LTM height (l)	2.12 ± 0.24	6	1.96 ± 0.22	9
LTM height (r)	2.09 ± 0.30	6	1.98 ± 0.18	9
LTM depth (l)	0.27 ± 0.16	6	0.24 ± 0.08	9
LTM depth (r)	0.41 ± 0.21	6	0.30 ± 0.12	9

[a] Left side of syrinx.
[b] Right side of syrinx.

taken. The longest diameter had an especially high loading on PC1a. Generally, female tracheas were shorter and more oval compared with the long, almost rounded tracheas of males (Table 3). The estimated tracheal volume was about 3,430 mm³ in males and 2,210³ mm in females.

Sex differences in PC1b, among others representing number of tracheal and bronchial rings (Table 2), might reflect body-size differences between males and females. To rule out effects of size on sexual differences in syringeal structures, we examined correlations between number of tracheal rings and: (1) length of the tracheosyringeal membrane; (2) number of modified tracheal rings; (3) number of connecting sheets; and (4) number of bronchial rings. None of these structures was significantly

TABLE 4. Sexual differences found in syringes stained with a cartilage-bone stain. Measures are expressed as number of rings. TSM, tracheosyringeal membrane.

Syrinx measures	Males $\bar{x}$ SD	*n*	Females $\bar{x}$ SD	*n*
General				
No. of tracheal rings	108.0 ± 5.1	11	101.8 ± 5.0	9
No. of bronchial rings (l)[a]	9.4 ± 0.8	13	8.8 ± 1.0	10
No. of bronchial rings (r)[b]	11.1 ± 1.2	13	10.0 ± 1.3	10
Bronchial rings with bone	3.8 ± 1.7	12	5.1 ± 2.2	10
Ventral side				
Ventromed. thickened rings	7.7 ± 0.9	14	6.7 ± 0.7	10
No. of connecting sheets	10.3 ± 1.3	14	9.7 ± 1.3	10
Dorsal side				
Length TSM	16.9 ± 1.2	14	14.8 ± 1.7	10
Max. width TSM	6.9 ± 0.7	14	5.4 ± 0.9	10

[a] Left side of syrinx.
[b] Right side of syrinx.

correlated with the number of tracheal rings. Thus, it is unlikely that sexual differences in these structures are a direct result of size differences between males and females.

Tracheal rings that are part of the syrinx are often modified in one or more ways. One such modification is a thickening of the rings over the ventral midline, seen in the most caudally positioned tracheal rings (Fig. 6). The number of thickened rings was highly correlated with PC1b, which showed a significant sex difference (Table 2). However, variation among females (six to eight rings) was completely within the range found in males (six to nine rings). The modified tracheal rings and rostrally positioned rings are connected by sheets of cartilage (Fig. 6). The number of connecting sheets had similar loadings on PC1b and PC4b but differed significantly between sexes only for PC1b.

The lateral tympaniform membranes (LTMs) are positioned in the lateral wall of the trachea between the first and second tracheal ring (Figs. 6 and 7). LTM measures of height and depth showed high loadings on PC2a (Table 1), a component that was not significantly affected by sex. Depth of the LTMs was significantly lateralized in male syringes (Wilcoxon matched-pairs test, $P = 0.0431$) with the right LTM being folded more into the lumen of the trachea (Table 3). In females, neither height nor depth of the LTMs showed bilateral asymmetry. An elastin band is situated lateral of the tracheal epithelium, starting caudal to the insertion of Mm. tracheolaterales onto the LTMs. The length of this elastin band differed significantly between males and females ($F = 6.34$, df = 1 and 10, $P = 0.03$). However, the position of the transition in tracheal epithelium, which is related to this elastin band, did not differ between the sexes (Table 5).

The tracheosyringeal membrane (TSM) is composed of a number of small oval-shaped membranes stretched between tracheal rings, which are reduced over the dorsal midline (Fig. 7). In some males and females the tracheal rings were lost altogether in the dorsal midline, the gap being closed by one large TSM. In males, the TSM had an average length of approximately 17 tracheal rings, individual means varying from 13 to 19 rings. The maximum width was reached at about T7. Females had less elongated TSMs of approximately 15 modified rings with a maximum width at about T5 (Table 4). The variation among females (13 to 17 rings) was within the range found in males. TSM length (expressed as the number of modified tracheal rings) had a high loading on PC1b (Table 1), whereas the position of its maximum width was mostly related to PC2b (Table 2). Only PC1b differed significantly between sexes. There was no correlation between TSM length and position of maximum width.

The trachea bifurcates caudally into the primary bronchi, which are constructed of a number of C-shaped rings. The medial tympaniform membranes are located between the dorsal and ventral ends of the bronchial rings (Figs. 6 and 7). The number of bronchial rings, both left and right (Table 4), was highly correlated with PC1b (Table 2), a component that differed significantly between males and females. A significant bilateral asymmetry in the number of bronchial rings occurred in both sexes, with the right bronchus consisting of more rings than the left (Wilcoxon test, $P = 0.002$ in males, $P = 0.008$ in females; Table 4). In males (but not females), the right bronchus was significantly longer and higher than the left one (Wilcoxon test, $P = 0.043$; Table 3). However, there was no effect of sex on PC3a, which had high loadings for left and right bronchial length and left bronchial height (Table 1). A significant bilateral asymmetry in bronchial volume was present in males (Wilcoxon test, $P = 0.043$), with the right bronchus being larger.

Discussion

Male and female Collared Doves differ significantly in several vocal characteristics of the perch-coo. Compared with males, females produce fewer and shorter coo bouts, and their coos contain less sound, tend to be less stereotyped, have a higher fundamental frequency, and have more overtones. Sex differences also occur in syrinx morphology. In general, the vocal apparatus of females appears to be a reduced copy of the one found in males. This is represented by sex differences in PC1b, representing the number of tracheal and bronchial rings, and PC1a, representing tracheal length. In addition to general size differences, more specific syringeal structures loaded highly on these principal components, e.g. longest tracheal diameter, number of ventromedially thickened rings, and length of the TSM. Bronchial length and height do not differ between the sexes but are bilaterally asymmetrical only in males.

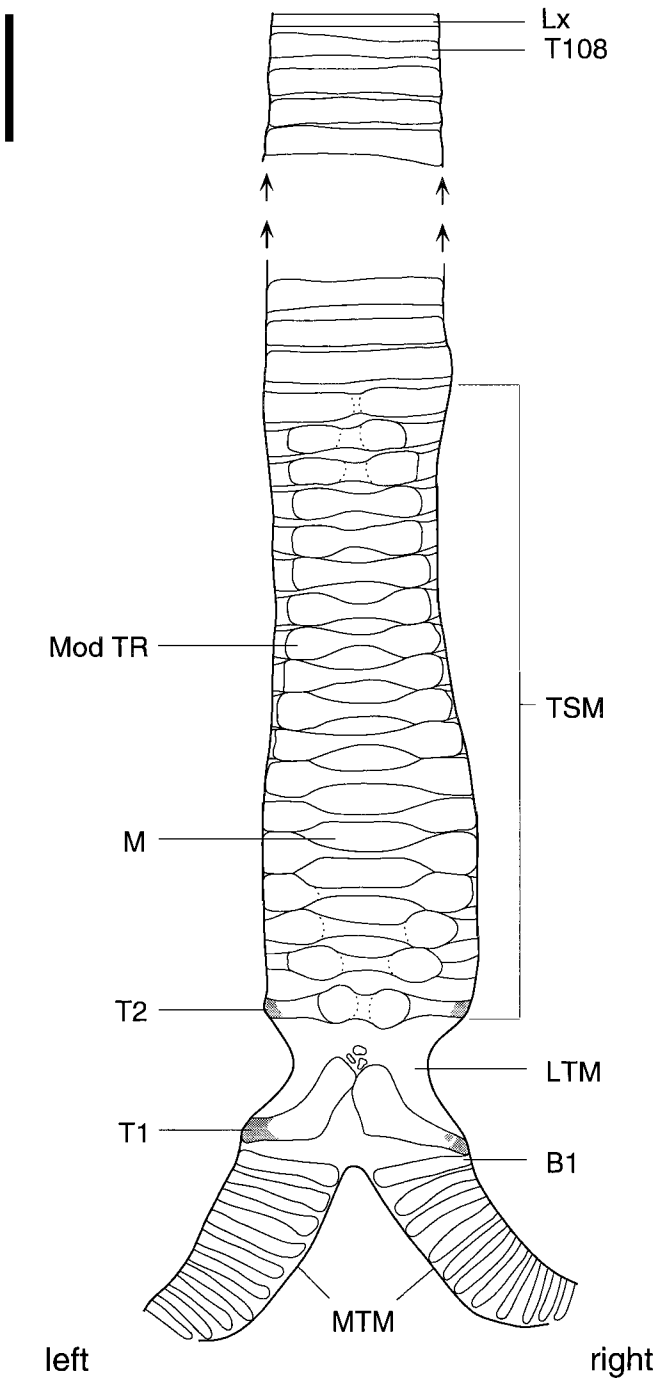

Fig. 7. Dorsal view of the Collared Dove syrinx with the Mm. sternotracheales and Mm. tracheolaterales removed. MTM, medial tympaniform membranes; LTM, lateral tympaniform membranes; TSM, tracheosyringeal membrane; Mod TR, modified tracheal rings (reduced over the dorsal midline); M, small membrane stretched between over the modified tracheal rings; T1, first tracheal ring; T2, second tracheal ring; B1, first bronchial ring; and Lx, larynx. Dark gray structures are ossified tissue. Scale bar = 2 mm.

TABLE 5. Sexual differences in horizontal sections of the syrinx, stained with Weigert-Van Gieson. Measures are expressed as number of rings.

	Males		Females	
Syrinx measures	$\bar{x}$ SD	n	$\bar{x}$ SD	n
Length elastin band	6.5 ± 1.7	4	4.8 ± 0.7	8
Transition trach. epithelium	5.0 ± 1.9	4	4.4 ± 0.7	8

Sex differences in vocalizations.—The perch-coo in Collared Doves usually is not categorized as "song," although it serves the biological functions of territorial defense and mate attraction (Cramp 1985). In the field, perch-coos are given mainly by males but also are produced by females (Hofstetter 1954). We obtained similar results in a laboratory environment where individuals were visually isolated from each other. Females produced perch-coos, but compared with males, females were not as active vocally. In some passerines the amount of song produced by females is strongly associated with seasonal or conflict-induced changes in testosterone levels (Kern and King 1972, Arcese et al. 1988). During the 16 weeks of our experiment, individual levels of vocal activity were relatively constant. The lack of intraindividual variation in the amount of cooing may be the result of the constant light and temperature regime, mimicking a constant environment. Changes in testosterone levels induced by conflicts were prevented by the isolated housing conditions. Nevertheless, distinct interindividual variation in vocal activity existed. Singing activity in captive female Song Sparrows (*Melospiza melodia*) was related to unusually high levels of aggressive behavior and high levels of androgens (Nice 1943). Administration of testosterone in Ringed Turtle-Doves increased both the number and length of coo bouts (Groothuis et al. 1993). Our results pointed in the same direction. In males, individuals producing the most and the longest coo bouts also were the most aggressive to their caretakers. In females, levels of aggression generally were low, except for one female that consistently produced male-like perch-coos. This suggests that intrasexual (and possibly also intersexual) variation in vocal activity and bout length is related to differences in testosterone levels.

Among passerines in which females do not sing regularly, song is often described as poorly developed and resembling that of immature males (Nice 1943, Arcese et al. 1988). This also is true for Collared Doves. Similar to juvenile males (Ballintijn and ten Cate unpubl. data), the perch-coos of females tended to be less stereotyped with more overtones and a lower sound percentage.

The number and nature of spectrotemporal characteristics examined in studies of sexual differences in vocalizations vary enormously. Nevertheless, most studies have analyzed one or more frequency aspects of the vocalizations. We measured the fundamental frequency because it was the most distinct frequency characteristic of the perch-coo. In most birds females produce higher frequencies than males (e.g. Zann 1984, Cavanagh and Ritchison 1987, Dooling et al. 1987, Bretagnolle 1989, Robisson 1992, Okanoya and Kimura 1993). However, a number of nonpasserines exhibit reversed sexual dimorphism in frequency (e.g. Taoka et al. 1989a, Rosenfield and Bielefeldt 1991, Farquhar 1993) that usually is explained by the fact that the female is the larger sex. The Collared Dove clearly belongs to the first category; females are smaller than males (Lachner 1965) and they produce higher fundamental frequencies (as indicated also by Ferianc *in* Cramp [1985]).

Sexual differences also have been reported for temporal structure of vocalizations. We documented that female Collared Doves produce a lower percentage of sound in a coo. In Zebra Finches (*Taeniopygia guttata*; Zann 1984) and Little Owls (*Athene noctua*; Exo 1984), which each give a single call at a time, call length is longer in males. In Swinhoe's Storm-Petrel (*Oceanodroma monorhis*), in which calls are given in a series, the elements are significantly shorter in females but the duration of pauses does not differ between the sexes (Taoka and Okumura 1990). The same is true for the song of the White-crowned Sparrow (*Zonotrichia leucophrys*; Baptista et al. 1993). In both species, as in the Collared Dove, females have a lower vocal output than males. In Bulwer's Petrel (*Bulweria bulwerii*; James and Robertson 1985a) and Cory's Shearwater (*Calonectris diomedea*; Bretagnolle and Le-

quette 1990), the temporal structure of vocalizations does not differ between sexes, whereas in Wilson's Storm-Petrel (*Oceanites oceanicus*; Bretagnolle 1989) and Cooper's Hawk (*Accipiter cooperii*; Rosenfield and Bielefeldt 1991), species in which females are larger than males, the sexual difference in element duration is reversed.

Few studies of sex differences in songs have quantified harmonic structure because female song is assumed to have the same pure-tonal quality as that of males (Gahr and Güttinger 1986, Hoelzel 1986, Baptista et al. 1993). However, in Northern Cardinals (*Cardinalis cardinalis*) sex differences occur in the "relative harmonic amplitude," with females having harmonics of higher amplitude than males (Yamaguchi and Marler pers. comm.). The harmonic structure of calls, if studied, has been described only qualitatively. For instance, in Band-rumped Storm-Petrels (*Oceanodroma castro*) and Manx Shearwaters (*Puffinus puffinus*), males produce "clear notes with a ringing vibrant quality that is lacking in the harsh sounds produced by females" (Brooke 1978, James and Robertson 1985b). We quantified harmonic structure by measuring the number of overtones with an amplitude of more than −70 dB, regardless of their relative amplitude. This method allows a quick and objective assessment of harmonic structure. The threshold level of −70 dB, approximately 10 dB above noise level, gave the same results as on-screen inspection of spectrograms and showed that female Collared Doves produce significantly more overtones than do males. A comparable situation, although not analyzed quantitatively, occurs in Swinhoe's Storm-Petrels. Female calls have a clear harmonic structure with several overtones, whereas male calls are broad-band sounds consisting of various frequencies (Taoka et al. 1989b). Playback experiments with synthetic calls have shown that the mere presence or absence of overtones is sufficient for discrimination between the sexes in this species (Taoka and Okumura 1990).

Spectrogram cross-correlations, which measure the stereotypy of vocalizations, have been used almost exclusively in studies on the development of song (e.g. Clarke et al. 1987, Nelson et al. 1995, Podos et al. 1995). We found that this technique is also useful in analyses of sexual differences in vocalizations. In Collared Doves, coo structure tends to be more stereotyped in males than in females. Similar results have been found in Northern Cardinals. In this species the sex of a singer is recognized based on its song. Spectrogram cross-correlations revealed that males have a better "syllable repetition accuracy" than females (Yamaguchi and Marler pers. comm.).

We have shown that at least seven vocal parameters of the perch-coo of Collared Doves differ between the sexes. Of these parameters, bout length is the best discriminator between males and females. However, if only one or a few coos are produced (by the sender) or heard (by the receiver), this parameter cannot be assessed easily. In such cases, only spectrotemporal features need to be used to distinguish between the sexes. In the DFA that included only spectrotemporal parameters, sound percentage had the highest discriminating value, followed by modulation percentage and fundamental frequency. However, these results do not provide insight into which parameters are used, or are best suited for use, by the receiver. Here, the capability of the receiver to detect certain differences plays an important role. Studies of Budgerigars (*Melopsittacus undulatus*) revealed that this species can detect a 10–20% change in the duration of an acoustic signal (Dooling 1982). In Collared Doves, the relative sex differences in the duration of the three elements listed above were 18.3%, 22.8%, and 30.0%, respectively. If the results for Budgerigars are an indication of the abilities of Collared Doves, then these differences are, except for element 3, on the verge of detection. Several studies have shown that birds are very sensitive to differences in the frequency of acoustical signals and are able to discriminate a 1% change in frequency (Dooling 1982). In Collared Doves, modulated elements are characterized by a discrete increase in frequency at the beginning of the element of about 110 Hz, corresponding to a change of about 21% (ten Cate 1992). This is well above the assumed detection ratio. Furthermore, playback experiments have indicated that territorial males perceive and respond differently to modulated compared with unmodulated perch-coos (Slabbekoorn and ten Cate 1996). Because the presence of modulations differs significantly between males and females, modulations may be one vocal cue used in sex recognition. The same may be true for the fundamental frequency of the perch-coo. Males and

females differ significantly in fundamental frequency, and this relative difference of approximately 15% also is likely to be perceived.

To summarize, characteristics of the perch-coo in female Collared Doves are in line with those of other female calls and songs. Together they indicate that sex differences in vocalizations show similar trends in passerines and nonpasserines. Furthermore, from a functional perspective, the magnitude of the sex differences found in our study suggests that some vocal parameters are used in sex recognition.

Sexual differences in the morphology of the syrinx.—Little information is available on sexual differences in the syrinx of passerines, although Myers (1917) posited that female passerines have weaker muscles, smaller labia, and less specialized cartilages. In nonpasserines, sexual dimorphism in the syrinx is most prominent in the Anatidae, namely in the presence of an asymmetrical syringeal bulla in males (Warner 1971, Platz 1974, Lockner and Youngren 1976). Besides the Anatidae, sexual differences in the structure of the syrinx have been studied in domestic fowl (Myers 1917, Appel 1929), owls (Miller 1934), and two species of *Columba* (Warner 1972).

The syrinx in the family Columbidae, including the Collared Dove, has been described by Warner (1972). Warner examined both sexes in *Columba livia* and *C. palumbus* and reported "no apparent difference in the syringeal structure between male and female." When studied in greater detail, however, we determined that the syringes of male and female Collared Doves are different, although not as markedly as in waterfowl (Warner 1971, Platz 1974, Lockner and Youngren 1976). In Collared Doves, as in domestic fowl (Myers 1917), the most prominent sexual difference in the syrinx is size. The female syrinx appears to be a smaller version of the male syrinx and is characterized by sexual differences in principal components that represent either the number of tracheal and bronchial rings, or tracheal length and diameter. This result may be expected, because sex differences in body size (Lachner 1965) are likely to be reflected in the size of the sound-producing organ. However, because the number of tracheal rings is not correlated with the size of other syringeal structures, size differences between males and females cannot account for sex differences in the number of ventrally modified tracheal rings, the size of the TSM, or the primary bronchi.

In the syringes of many birds, the most caudal tracheal rings are modified and fused into a "tympanic box" (King 1989). A tympanum is not present in Collared Doves, but the ventrally modified tracheal rings form a distinct component of the syrinx (Ballintijn et al. 1995). The high loading of the number of ventromedially modified tracheal rings on PC1b suggests that male Collared Doves have more ventromedially modified rings than do females. A comparable sexual difference is found in the number of rings forming the tympanum in the syrinx of domestic fowl (Myers 1917). However, the latter result could not be confirmed by Appel (1929).

In the Collared Dove, like in the Ring-necked Dove (*Streptopelia capicola*; Rüppel 1933), tracheal rings are modified dorsally to form a tracheosyringeal membrane (Ballintijn et al. 1995). This type of membrane is typical for columbiforms, although size and shape of the membrane vary between species (King 1989). We showed that tracheosyringeal membrane length is highly correlated with PC1b and therefore is likely to differ between male and female Collared Doves. No data on sex differences in this membrane are available for other columbiforms.

In several strigiforms, the number of bronchial rings is higher in males than in females (Miller 1934). In Collared Doves, the principal component representing the number of rings in the left and right bronchus differs between the sexes, although both sexes show the same degree of asymmetry in the number of bronchial rings. Asymmetry in the number of bronchial rings occurs in many species (Rüppel 1933, King 1989), although these studies did not consider differences between the sexes. Miller (1934) also found differences between the sexes in the bronchial diameter of some strigiforms. Despite sex differences in trachea length (this study) and body size (Lachner 1965), we found no indication of sexual dimorphism in either the length or height (diameter) of the primary bronchi. Nevertheless, male syringes are distinctly bilaterally asymmetrical in size of the bronchi, whereas female bronchi are more symmetrical. Miller (1934) found similar results in strigiforms, and in female anatids syringes are bilaterally symmetrical (Warner 1971, Platz 1974, Lockner and Youngren 1976).

The cause of vocal sex differences.—At least two models have been developed to explain sound production in birds. Most of this research is based on the "classical" model (Brackenbury 1982, Gaunt and Gaunt 1985, Nowicki and Marler 1988), which considers vibration of the medial tympaniform membranes (MTMs) to be the prime sound source. However, because this model fails to explain the production of pure tones (Casey and Gaunt 1985, Gaunt and Gaunt 1985), an alternative was proposed by Gaunt et al. (1982). Their study of Ringed Turtle-Doves led to the hypothesis that sound is generated by forcing air through a small slit in a manner analogous to a whistle. Nowicki (1987) questioned the validity of the "whistle" model, suggesting instead that pure tones are produced as sounds with a harmonic structure followed by selective attenuation of overtones. Data on syrinx structure in Collared Doves also suggest that vibration of the MTMs, rather than a whistle, is the source of sound production in *Streptopelia* (Ballintijn et al. 1995). We will therefore assume that sound is produced primarily by the vibration of the MTMs. A second assumption is that the mechanism of sound production is similar in male and female Collared Doves, because their syringes have the same basic structure. This is in contrast to Mallards, whose elaborate sexual dimorphism in syrinx morphology has led to distinctly different sound-producing mechanisms in males and females (Lockner and Youngren 1976).

If sounds are produced by the vibration of the MTMs, then frequency characteristics of the sound are determined by the size of the membranes (Würdinger 1970, Abs 1980) and the applied tension (Casey and Gaunt 1985). We did not measure the size of the syringeal muscles and therefore could not assess if males and females differ in the tension that can be applied to the membranes. However, because the MTMs are stretched between the open ends of the bronchial C-shaped rings (Ballintijn et al. 1995), their size can be estimated from the bronchial width and length. Although male Collared Doves tend to have larger MTMs than females, MTM size is statistically similar in both sexes and thus cannot account for the sex differences in the fundamental frequency of the perch-coo. Nonetheless, it can be hypothesized that not only membrane size, but also membrane structure determines the fundamental frequency of vocalizations. If this is true, then sex differences in membrane structure may cause sex differences in frequency. Detailed examination of membrane structures in males and females may shed light on this issue.

Theoretically, the bilateral asymmetry in bronchus size enables male Collared Dove to produce two harmonically unrelated sounds at the same time. Interaction of the "two voices" might lead to the production of complex sounds (Gaunt and Gaunt 1985, Nowicki and Marler 1988). However, at present it is unknown whether Collared Doves can use their syrinx in such a manner, and if so, how this would affect the spectrotemporal structure of the vocalization.

The harmonic structure of a vocalization is not determined in the primary bronchi by characteristics of the MTMs, but by tracheal resonances that selectively attenuate the acoustical energy of certain frequency bands (Nowicki 1987, Nowicki and Marler 1988). Therefore, sex differences in trachea shape and size may lead, via changing resonance properties, to sexual differences in the harmonic structure. In Collared Doves, not only are trachea size and shape likely to differ between the sexes, but also the length of the TSM. The effect of variation in TSM size is difficult to assess because its function is unknown. Owing to its structure and position in the tracheal wall, the TSM is likely to influence resonance characteristics of the trachea. Nevertheless, as long as the precise mechanism of vocal filtering is unclear, it will be difficult to explain sexual differences in the harmonic structure by differences in tracheal structure.

At least two other explanations exist for the presence of sex differences in harmonic context, which also might explain the tendency for sex differences in stereotypy. In Song Sparrows (Podos et al. 1995) and Collared Doves (Ballintijn and ten Cate unpubl. data), vocalizations change during ontogeny from rather variable sounds with harmonics into stereotyped, puretonal vocalizations. Song Sparrows increase their control over the syringeal configuration and the coordination between syringeal output and vocal tract resonances by motor "practice" (Podos et al. 1995). Because female Collared Doves coo less than males, perhaps they have had less opportunity to acquire optimal control over their vocal apparatus, resulting in less "mature" coos. In addition, differences between sexes in hormone levels may cause differences in cooing. Groothuis et al. (1993) changed the vocaliza-

tions of young Ringed Turtle-Doves into "adult-like" vocal displays by administration of testosterone. Because the perch-coos of female Collared Doves resemble the coos of immature males (Ballintijn and ten Cate unpubl. data), sex differences in vocal structure might be related to differences in testosterone levels affecting not just syrinx structure, but also neural control centers. Although the precise linkage between sex differences in vocalizations and syringeal morphology still remains to be solved, our study demonstrates the plausibility that morphological aspects may contribute to sexual dimorphism in vocalizations.

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