

SOUND PRODUCTION IN THE COLLARED DOVE: A TEST OF THE ‘WHISTLE’ HYPOTHESIS

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Summary

The mechanism of sound production in the collared dove *Streptopelia decaocto* was studied to test the validity of the ‘whistle’ model and to analyze the role of vocal tract resonances. In this study, the vocalizations of six male adult doves were recorded both in normal air and in a mixture of 80% helium and 20% oxygen (heliox). Depending on the way in which the syrinx operates, the spectral structure of the vocalizations is expected to show specific changes in heliox. The effects of heliox differed substantially depending on the type of vocal element. Except for a significant decrease in amplitude, unmodulated elements, i.e. elements with a constant frequency, were relatively unaffected by heliox. In contrast, modulated elements, i.e. elements with an abrupt increase in frequency, showed a gradual increase in frequency with increasing helium concentration. This specific increase in frequency stopped when the modulation frequency was 1.5 times the base frequency, even when the helium concentration was increased further. In some individuals, a frequency band of half the base frequency was also observed. In general, the

proportion of modulated elements also showed a significant decrease. The lack of change in the fundamental frequency of the unmodulated elements and in the base frequency of the modulated elements indicates that these vocalizations are not produced like a whistle. It is more likely that they are the result of vibration of the syringeal membranes. Generally, vocal tract resonances do not play an active role in the modification of vocalizations, although they might enhance the fundamental frequency passively. The results suggest that the almost pure tonal vocalizations are produced as such in the syrinx and undergo limited modification when passing through the vocal tract. The effect of heliox on the modulation frequency suggests (1) that different sound-producing mechanisms may underlie different types of vocalizations, and (2) that resonance properties of the vocal system may be involved in the production or modification of the modulation frequency.

Key words: sound production, vocalization, birdsong, non-songbird, helium, vocal tract resonance, *Streptopelia decaocto*, collared dove.

Introduction

The production of bird vocalizations is a complex process that is still not fully understood. Three models, not necessarily mutually exclusive, have been proposed to explain the generation of sound in the syrinx of birds (reviewed by Gaunt and Gaunt, 1985; Gaunt, 1987; Nowicki and Marler, 1988).

The ‘classical’ model, based on work by Greenwalt (1968) and Stein (1968), assumes that syringeal membranes are set into a cyclic vibration by two opposing forces: Bernoulli forces created by the airflow, and elastic restoring forces of the membrane itself (Brackenbury, 1979). Alternatively the ‘pulse tone’ model proposes that the syringeal membranes operate like a valve, which occludes the tracheal lumen until it is forced open by the increasing air pressure behind it (Beebe, 1925; Klatt and Stefanski, 1974; Gaunt and Gaunt, 1985; Gaunt, 1987). Both the ‘classical’ and ‘pulse tone’ models involve the mechanical vibration of syringeal membranes and may be

considered as the extreme ends of a continuum, with intermediate forms being possible (Gaunt and Gaunt, 1985; Gaunt, 1987).

In contrast to the first two models, the third model is based primarily on aerodynamic principles. By forcing the airflow at high speed through a constriction in the syrinx, vortices are created in the airflow, which in turn result in a stable pattern of changes in air pressure as in some whistles (Chanaud, 1970). Gaunt *et al.* (1982) proposed this ‘whistle’ model to account for the production of pure-tone vocalizations in the ring dove *Streptopelia risoria*. A whistle is capable of producing a relatively pure tone (Chanaud, 1970; Casey and Gaunt, 1985) which, according to theoretical models, cannot be produced by freely oscillating edge-clamped membranes (Casey and Gaunt, 1985; Gaunt and Gaunt, 1985).

In principle, the fundamental frequency of a whistle or other musical wind instrument is determined by resonances that

stabilize the acoustic disturbance in the airflow (Chanaud, 1970). Consequently, altering the resonance frequency of a whistle, for instance by replacing atmospheric nitrogen with helium, will always lead to a shift in its fundamental frequency (Nowicki and Marler, 1988). In contrast, if the primary sound sources are vibrating membranes, which are not coupled or only loosely coupled to a resonance frequency, as in human speech (Rossing, 1989), heliox will have no effect on the fundamental frequency of a vocalization (Beil, 1962; Holeywell and Harvey, 1964). Nine songbird species (Nowicki, 1987) and one psittacine species (Brittan-Powell *et al.* 1997) have been recorded in a heliox. In none of the species was a shift in the fundamental frequency of pure tones observed (Brittan-Powell *et al.* 1997; Nowicki, 1987). Therefore, it seems likely that sound production in birds involves the mechanical vibration of syringeal membranes instead of the aerodynamic principle of a whistle (Nowicki, 1987; Nowicki and Marler, 1988). Recently, this has been confirmed by a study on the biomechanics of sound generation (Goller and Larsen, 1997). Nevertheless, no doves or pigeons, species for which the 'whistle' model was elaborated in detail (Gaunt *et al.* 1982), have yet been recorded in a heliox.

In addition to the primary mechanisms of sound generation, the role of vocal tract resonances is also still debated. For many years it has been assumed that modulations of bird vocalizations are entirely source-generated (Greenwalt, 1968; Casey and Gaunt, 1985; Gaunt, 1987; Brackenbury, 1989). In contrast, Nowicki (1987) suggested that vocal tract resonances can track syringeal output actively, thereby enhancing certain frequency bands while dampening others (Nowicki, 1987; Nowicki and Marler, 1988). This process shows great similarity to the filtering properties of the human vocal tract (Rossing, 1989). Studies in birds showed that the resonance properties of the vocal tract may be altered by posture and by throat and beak movements (Hausberger *et al.* 1991; Westneat *et al.* 1993). However, in budgerigars *Melopsittacus undulatus*, the active use of vocal tract resonance to modulate call structure could not be confirmed (Brittan-Powell *et al.* 1997).

In the present study, the sound-producing and modulating mechanisms in a non-songbird, the collared dove *Streptopelia decaocto*, were analyzed. The collared dove is closely related to the ring dove, which was used by Gaunt *et al.* (1982) to develop the 'whistle' model. Its vocalizations, called coos, are relatively simple and stereotypic (Gürtler, 1973; ten Cate, 1992). As in the ring dove (Gaunt *et al.* 1982), coos often show a more-or-less pure tonal character (Gürtler, 1973). Nevertheless, in adult females (Ballintijn and ten Cate, 1997a) and young males, multiple harmonics are present (Ballintijn and ten Cate, 1997b). In young males, the number of harmonics decreases significantly during development, although a few low-amplitude harmonics may remain in adult male cooing (Ballintijn and ten Cate, 1997a). The extensive information about both the structure of vocalizations and syringeal morphology (Ballintijn *et al.* 1995; Ballintijn and ten Cate, 1997a,b) makes the collared dove a good model

species to study further the validity of the 'whistle' model and to examine the role of vocal tract resonances in sound production.

The aim of the present study was twofold. First, to test the validity of the 'whistle' model. If the vocalizations of the collared dove are produced by a whistle-like mechanism, there should be strong coupling between the sound source and resonance frequency, resulting in a significant increase in fundamental frequency when vocalizing in a mixture of air and helium (heliox). Second, to examine the role of vocal tract resonances in the production or modulation of bird vocalizations. If vocal tract resonances play no role, the structure of vocalizations should be unaffected by heliox. Otherwise, changes in the amplitude of the fundamental frequency and possible harmonics are to be expected.

Materials and methods

Experimental animals

Six adult male collared doves *Streptopelia decaocto* (Aves; Columbidae) were used in this study. Doves were housed individually in wooden cages (70 cm×60 cm×60 cm) with a single perch and a wire mesh front. Food and water were provided *ad libitum*. Light conditions were maintained on a 13 h:11 h L:D photoperiod.

Experimental arrangement

Dove calls were recorded in a cage similar to their home cage. The experimental cage was lined with 2 cm thick acoustic foam on the ceiling and back wall to reduce sound reflection. The front of the cage could be closed with an acrylic front. A rubber lining minimized leakage of heliox. The volume of the cage was approximately 280 l.

There were six small openings (diameter 1 cm) in the side walls of the cage. In the left wall, there were three openings close to the ceiling, and in the right wall there were three openings close to the floor. Initially, the three high openings were used as entrance holes for the gas mixture, while the three low ones were used as exit holes. However, during the experiments, these settings were changed to two high and one low entrance hole, with the remaining openings sealed (see Table 1). In this way, better gas mixing and a higher helium concentration, could be achieved inside the cage (Table 1). Through the entrance holes, the cage could be filled with either normal air (using a ventilator) or heliox (a gas mixture of 80 % helium and 20 % oxygen; AGA gas BV, Amsterdam), which was released from a pressurized tank using a flow regulator (see Table 1 for flow rates).

A microphone (Sennheiser MKH 50, P48) was placed half-way through an opening in the acrylic front, which was lined with a rubber coating to avoid leakage. The microphone and the head of the dove while sitting on the perch were at approximately the same height. The microphone was connected to a tape recorder (Sony TC-D5 PRO II).

Changes in resonance frequency were monitored using a toy flute inside the experimental cage. The toy flute was positioned

Table 1. *Experimental settings and the percentage shift in the fundamental frequency of the toy flute*

Individual	Entrance holes	Exit holes	Pre-experimental flow rate (l h ⁻¹)	Experimental flow rate (l h ⁻¹)	Fundamental frequency of toy flute in air (Hz)	Fundamental frequency of toy flute in heliox (Hz)	Shift in fundamental frequency of toy flute (%)
118	3 high	3 low	1120	560	1546	2049	32.5
008	3 high	3 low	1275	560	1547	2301	48.7
111	3 high	3 low	1275	560	1572	2152	36.9
178	2 high, 1 low	1 low	1275	1120	1558	2430	56.0
160	2 high, 1 low	None	1275	560	1614	2424	50.2
015	2 high, 1 low	None	1275	1120	1618	2459	52.0

in such a manner that it could be operated from outside the cage using a turkey baster.

Procedure

Doves were placed in the experimental cage and left there for 3–10 days to habituate to the new surroundings. Normal air was circulated through the cage using the ventilator (flow rate 2240 l h⁻¹).

Control and heliox recordings were performed on two consecutive days. On both days, recordings were made 1.5–2.5 h after light onset (08:00 h), as collared doves are most active vocally in this period (M. R. Ballintijn, personal observation.). During the first day, recordings were made from coos produced in normal air. On the second day, recordings of the toy flute were made in normal air (10 replicates). The fundamental frequency of the toy flute is determined by tube resonances and will thus give an indirect measure of the helium concentration in the experimental cage (Nowicki, 1987). Next, during a 15 min pre-experimental period, the cage was flushed with heliox at a relatively high flow rate (Table 1) to force the normal air out of the cage. After the pre-experimental period, the toy flute was recorded again (10 replicates), and flow rate was lowered for the duration of the experiment. In two experiments (individuals 178 and 015), flow rate was kept at a relatively high level throughout both the pre-experimental period and the experiment itself in order to obtain a higher helium concentration inside the cage (Table 1). During the experiment, the toy flute was recorded every 30–45 min (each time with 10 replicates).

Analysis

As in many doves, three coo types can be distinguished in the collared dove (Goodwin, 1954) on the basis of context, visual display (Cramp, 1985) and acoustic differences (ten Cate, 1992): the perch-coo, bow-coo and nest-coo. The perch-coo was the coo type that was produced most often during the recordings and was therefore used in the analysis. However, anecdotal observations concerning the bow-coo and nest-coo suggested that the effects of heliox were similar for all three coo types. The coo of the collared dove consists of three elements. Each element can have one of two frequency profiles, ‘unmodulated’ or ‘modulated’. Unmodulated

elements have a relatively constant frequency, although on a sonogram they might be slightly bow-shaped (see Fig. 1 for examples). Modulated elements have an abrupt, sometimes stepwise, increase in frequency at the beginning of an element. At the end of the element, the frequency gradually decreases to its starting value (see Fig. 1 for examples; for details, see Gürtler, 1973; ten Cate, 1992). Coos are produced in sequences, which are referred to as coo bouts.

All perch-coo bouts were used to calculate the vocal activity level (mean number of coo bouts produced per hour), bout length (the number of coos in a series) and modulation percentage per bout (the percentage of elements in a bout that occurred in the modulated form) during control and heliox recordings. Coo bouts produced during the 15 min pre-experimental period were excluded from these calculations because the helium concentration inside the cage was still variable and the experimenter, who operated the toy flute twice within this short period, might have had a disturbing effect on the doves.

The effects of heliox on unmodulated and modulated elements were analyzed separately. For the analysis of unmodulated elements, all second elements of the second or third coo of each coo bout were selected, up to a maximum of 20 unmodulated elements for both control and heliox recordings. This specific element was chosen because it is usually unmodulated, relatively long and stable in frequency. As some individuals produced fewer coo bouts than others, set size varied (control recordings, 15–20 unmodulated elements; heliox recordings, 9–15 unmodulated elements). For the analysis of modulated elements, all first elements of the second and third coo, if modulated, were selected, again up to a maximum of 20. In this case, the first element rather than the second was chosen because it showed the highest proportion of modulations. Owing to individual variation in vocal activity and modulation percentage, set size varied (control recordings, 10–20 modulated elements; heliox recordings, 15–20 modulated elements). Power spectra were generated from all selected elements (sampling rate, 12.5 kHz; 4096-point power transforms; frequency resolution, 3 Hz).

Power spectra were analyzed in a standardized manner using the SIGNAL sound-analysis system (Engineering Design). First, the fundamental frequency of the element was

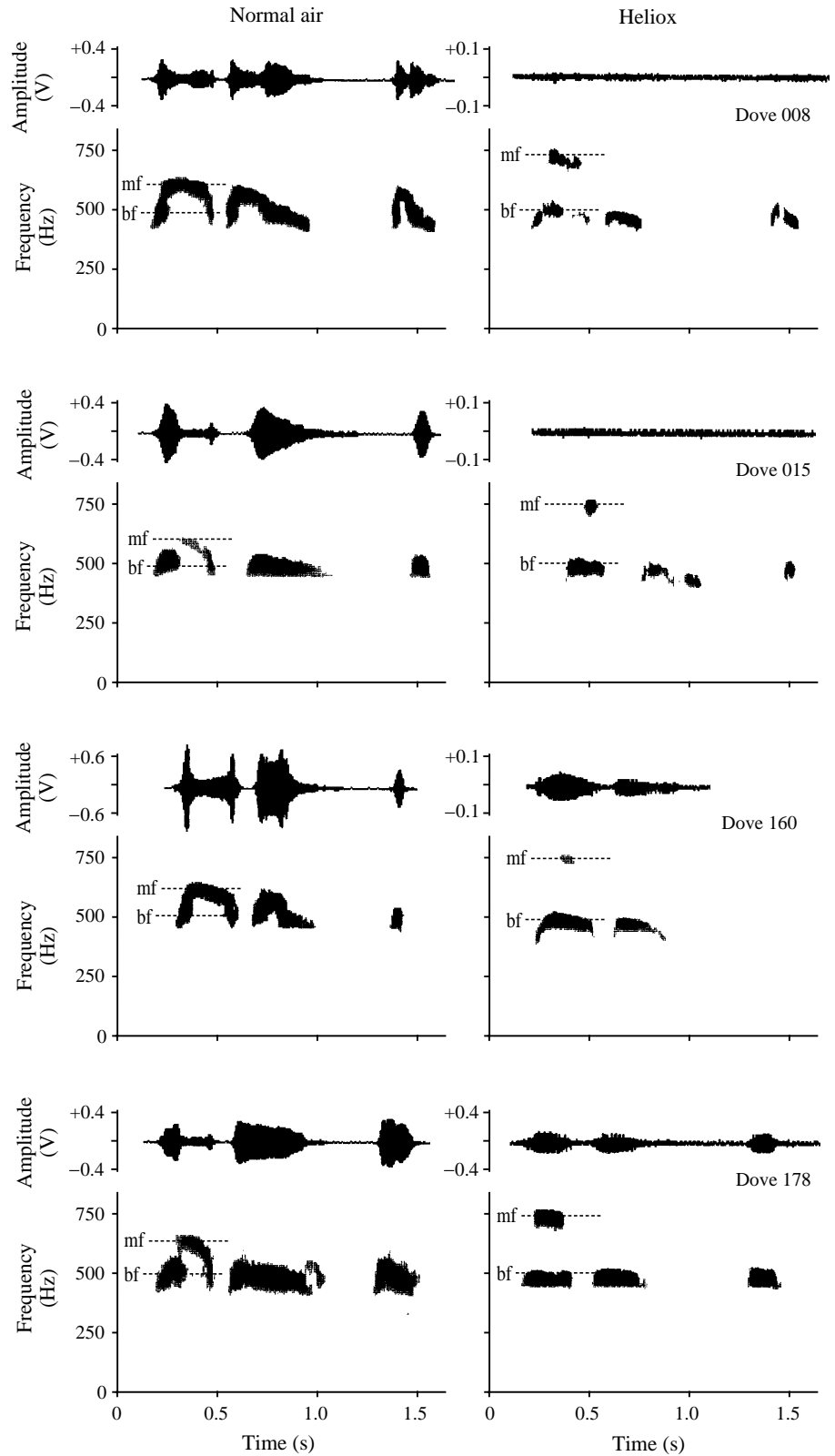


Fig. 1. Sonograms and amplitude envelopes of perch-coos produced in normal air and in heliox by four different collared doves. Note that the scale of the amplitude axis varies between normal air and heliox because of the large amplitude difference between the two conditions. In normal air, individual 008, all three elements are modulated; individual 160, the first and second element are modulated; individuals 015 and 178, only the first element is modulated. In heliox, modulations are only produced on the first element of the perch-coo. The perch-coo of individual 160 consists of two elements only in heliox. Two measures can be taken of the modulated elements: base frequency (bf) and modulation frequency (mf). In heliox, two parallel frequency bands continuous in time are visible in the modulated element, while in normal air there is hardly any overlap in time between the frequency bands.

determined by measuring the frequency at peak amplitude in a range between 400 and 650 Hz. The power spectrum of an unmodulated element shows one distinct amplitude peak, which is related to the fundamental frequency of the element.

Next, as harmonics are multiples of the fundamental frequency, the amplitude and frequency of an overtone were determined by measuring the peak amplitude in a section of the power spectrum in which an overtone could be expected (section = n

\times fundamental frequency ± 50 Hz, for $n=2-4$, where n is the number of the harmonic). However, as preliminary analyses had shown that, in heliox, frequency peaks were sometimes present at 0.5 and 1.5 times the fundamental frequency, peak amplitudes were also measured in sections for which $n=0.5-4.5$. For modulated elements, the analysis was performed separately for the base frequency and the frequency of the modulation (Fig. 1). Both base and modulation frequency were determined by measuring the two amplitude peaks visible in the power spectrum of a modulated element. One amplitude peak relates to the base frequency (lowest frequency), while the other relates to the modulation frequency (higher frequency). In addition, a noise level was defined as the mean amplitude in the frequency range between 3000 and 5000 Hz. In this range, it is rare to find harmonics in male perch-coos (Ballintijn and ten Cate, 1997a). The harmonic structure was defined as the number of harmonics with amplitudes 10 dB above the noise level.

If there is strong coupling between the sound source and resonance frequency, there will be a shift in the fundamental frequency of the vocalization in helium. In this case, the proportional shift in the fundamental frequency of the toy flute may be used to calculate the frequency to which the fundamental frequency of the dove coos would shift (Brittan-Powell *et al.* 1997). It should be kept in mind that such a shift in heliox depends on the geometrical structure of the resonating instrument, which clearly differs between a toy flute and a bird. Nevertheless, the shift in fundamental frequency of the toy flute may be used as an indication, or approximation, of the shift in fundamental frequency of the dove coos. To examine the presence of such a shift, the mean amplitudes of the unmodulated element produced in normal air and heliox in a frequency range of 100 Hz around this hypothetically shifted fundamental frequency were compared.

Statistics

Shapiro Wilks tests showed that all parameters were normally distributed, except for modulation percentage. The effects of heliox on vocal activity and bout length were tested using a paired t -test. A paired t -test was also used to determine the effect of heliox on the fundamental frequency and its amplitude of unmodulated elements and the toy flute and on the amount of energy in the hypothesized 100 Hz frequency band. The effects of heliox on aspects of frequency modulations were tested for individuals separately, as there were only four individuals producing these modulations in heliox. The effects of heliox on the modulation percentage were tested using a Wilcoxon matched-pairs signed-ranks test, while its effects on the base and modulation frequency, and their amplitudes, were tested using individual t -tests.

Results

During the experiments, the fundamental frequency of the toy flute showed a significant increase (Figs 2A, 3; $t=-11.82$, $P<0.001$). This means that by flushing the cage with a mixture

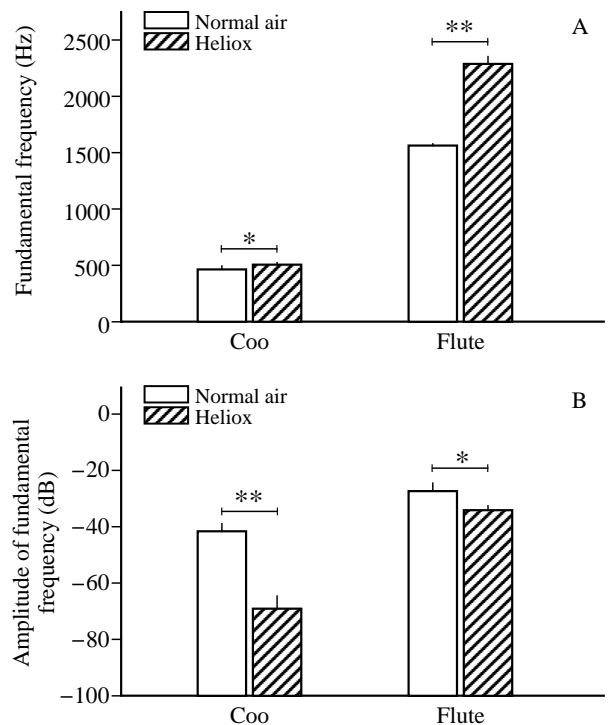


Fig. 2. The effect of heliox on the fundamental frequency (A) and its amplitude (B) of both unmodulated collared dove coos and the toy flute. Values are means + s.e.m. ($N=6$, $*P<0.05$, $**P<0.001$).

of 80% helium and 20% oxygen a shift in the resonance frequency was achieved of, on average, 46% (Table 1; Figs 2A, 3). Furthermore, the amplitude of the fundamental frequency of the toy flute decreased significantly by approximately 6 dB (Fig. 2B; $t=3.52$, $P=0.017$).

The mean vocal activity level of the doves during the control recordings, 19.7 ± 9.8 coo bouts h^{-1} (mean \pm s.d., $N=6$), did not differ significantly from the activity level observed in heliox (17.2 ± 8.9 coo bouts h^{-1} , $t=0.60$, $P=0.573$). Bout length, in contrast, showed a significant increase in heliox, from 7.9 ± 1.0 to 9.1 ± 1.0 coos per bout (mean \pm s.d.; $N=6$, $t=-5.54$, $P=0.003$).

The effect of heliox on unmodulated elements

In the power spectra of unmodulated elements produced in normal air, the first harmonic, i.e. the fundamental frequency, appeared at a mean value of 484 Hz and had a mean amplitude of -42.3 dB. Changing the atmosphere from normal air to heliox resulted in a slight, but significant, increase in the fundamental frequency by 3.6% (Figs 2A, 4; Table 2; $t=-3.33$, $P=0.021$). The amplitude of the fundamental frequency showed a decrease of approximately 29 dB (Figs 2B, 4; Table 2; $t=8.97$, $P<0.001$). The decrease in amplitude was present in the first coos produced in heliox (see Fig. 5). Furthermore, there was a slight, but also significant, decrease in mean acoustic energy in the 100 Hz frequency band around the hypothetically shifted fundamental frequency from -88.8 ± 4.0 dB in normal air to -92.8 ± 6.8 dB in heliox (mean \pm s.d.; $N=6$, $t=2.99$, $P=0.030$).

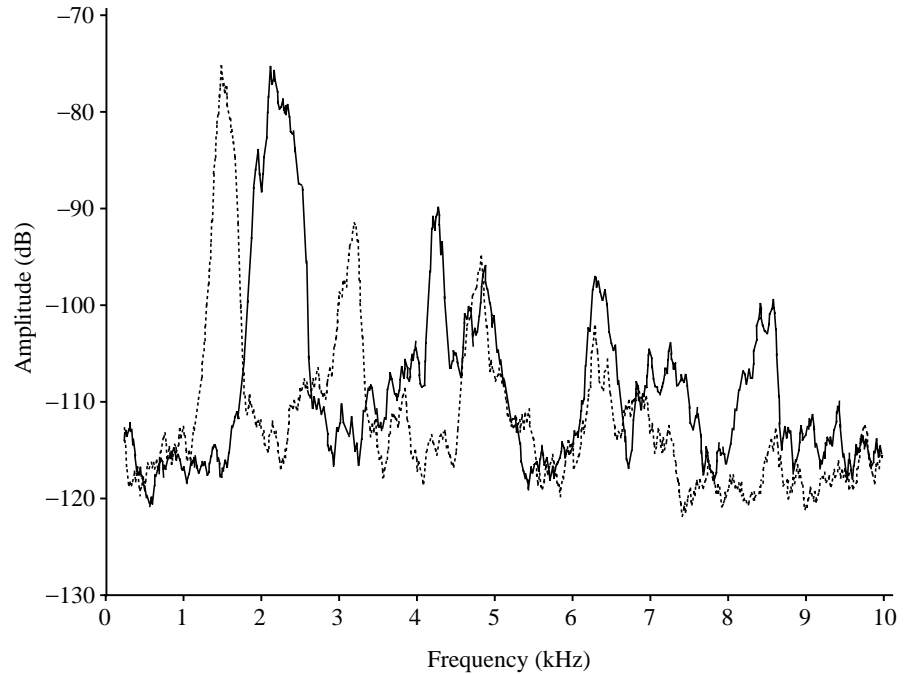


Fig. 3. Power spectra of the toy flute in both normal air and heliox (25 kHz sample rate, 10 kHz analysis range, 2048 point transforms, 12 Hz frequency resolution). Each power spectrum is a mean calculated over the six experiments. Dotted line, normal air; solid line, heliox.

In addition to the fundamental frequency, 1.2 ± 0.5 harmonics were found in unmodulated elements produced in normal air, appearing as the second (972 ± 75 Hz) and/or third (1482 ± 36 Hz) harmonic in the power spectra (mean \pm s.d.; Fig. 4; Table 2). However, with amplitudes of -77.1 ± 3.8 dB and -81.0 ± 2.9 dB, respectively, they were much weaker than the fundamental frequency. In heliox, the number of harmonics decreased significantly to 0.4 ± 0.5 (Fig. 4; Table 2; mean \pm s.d.; $N=6$, $t=5.59$, $P=0.003$). The few harmonics present in heliox were approximately twice (1003 ± 13 Hz) or three times

(1510 ± 12 Hz) the value of the fundamental frequency (501 ± 15 Hz).

The effect of heliox on frequency modulations

Five of the six individuals produced so-called frequency modulations. In normal air, the mean modulation percentage was 27.9 ± 30.3 % (mean \pm s.d., $N=6$). In heliox, this percentage decreased by 14.4 % to 13.5 ± 18.5 %. In four individuals, the decrease in modulation percentage was significant (individual 008, $Z=-4.82$, $P<0.001$; individual

Table 2. Frequency and amplitude of unmodulated elements of perch-coos of collared doves in normal air and heliox

Individual	Mixture	F1 (Hz)	A1 (dB)	F2 (Hz)	A2 (dB)	F3 (Hz)	A3 (dB)	F4 (Hz)	A4 (dB)	Noise (dB)
008	Normal	511	-42.4	1023	-84.9	1526	-84.6	2039	-93.2	-94.6
	Heliox	521	-78.4	1039	-95.6	1561	-96.4	2071	-97.1	-99.7
015	Normal	429	-44.7	846	-77.2	1289	-92.2	1715	-93.3	-94.2
	Heliox	466	-80.9	935	-93.7	1392	-94.4	1853	-93.2	-97.1
111	Normal	481	-49.0	971	-86.5	1438	-83.8	1919	-92.0	-93.8
	Heliox	501	-78.2	991	-93.8	1510	-94.3	1996	-95.8	-98.4
118	Normal	511	-40.1	1023	-71.7	1528	-78.6	2049	-88.6	-90.4
	Heliox	511	-58.0	1012	-77.4	1524	-86.1	2038	-86.9	-95.5
160	Normal	491	-38.4	987	-77.6	1479	-82.2	1965	-93.5	-94.4
	Heliox	505	-59.4	1014	-91.9	1514	-86.6	2013	-94.9	-97.3
178	Normal	482	-39.3	968	-82.2	1446	-80.6	1922	-91.3	-93.2
	Heliox	502	-73.5	993	-92.8	1515	-92.1	1996	-96.2	-98.4

F1, frequency of the first harmonic; A1, peak amplitude of the first harmonic; F2, frequency of the second harmonic; A2, peak amplitude of the second harmonic, etc.

Note that in normal air the third and fourth harmonics, and in heliox the second, third and fourth harmonics, are only a few decibels higher than the noise level. According to the definition given in Materials and methods, only harmonics with an amplitude of 10 dB above noise level are considered as harmonics.

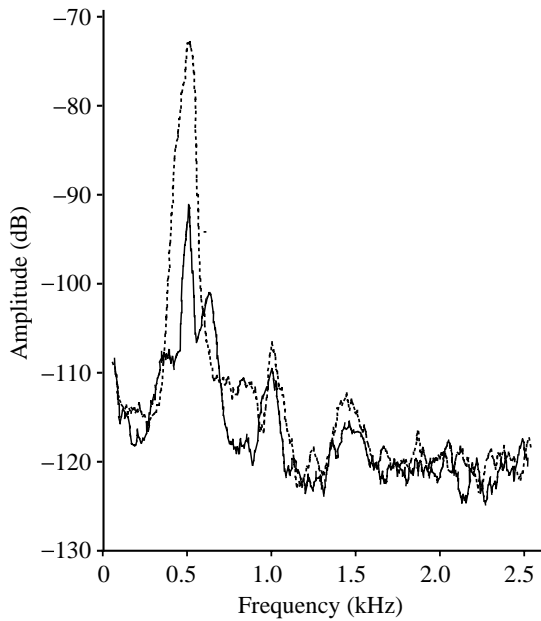


Fig. 4. Power spectra of unmodulated elements of perch-coos by collared doves in normal air and heliox (12.5 kHz sample rate, 2.5 kHz analysis range, 4096 point transforms, 3 Hz frequency resolution). Each power spectrum is a mean calculated over six individuals. Dotted line, normal air; solid line, heliox.

118, $Z=-3.24$, $P=0.001$; individual 160, $Z=-5.08$, $P<0.001$; and individual 178, $Z=-4.17$, $P<0.001$), while one individual showed a significant increase (individual 015, $Z=-2.22$,

$P=0.027$). Not only did the average modulation percentage decrease, but the distribution of frequency modulations over the elements of a coo also changed significantly. In normal air, modulations were found on all three elements, although individual differences were present. In heliox, frequency modulations were only present on the first element and not on the second or third (Fig. 6).

Not only was the occurrence of frequency modulations affected by heliox, but the spectrotemporal structure of the modulations also changed. In normal air, a modulated element started with a fundamental frequency of, on average, 500 Hz, which is called the base frequency (Fig. 1, normal air). Shortly after the start of the element, the fundamental frequency increased abruptly to approximately 580 Hz, the so-called modulation frequency. In general, there was relatively little overlap in time between the base and modulation frequency (Fig. 1, normal air). Both frequencies were visible as distinct peaks in the power spectrogram (Fig. 7; Table 3). In two individuals, the amplitude of the base frequency was

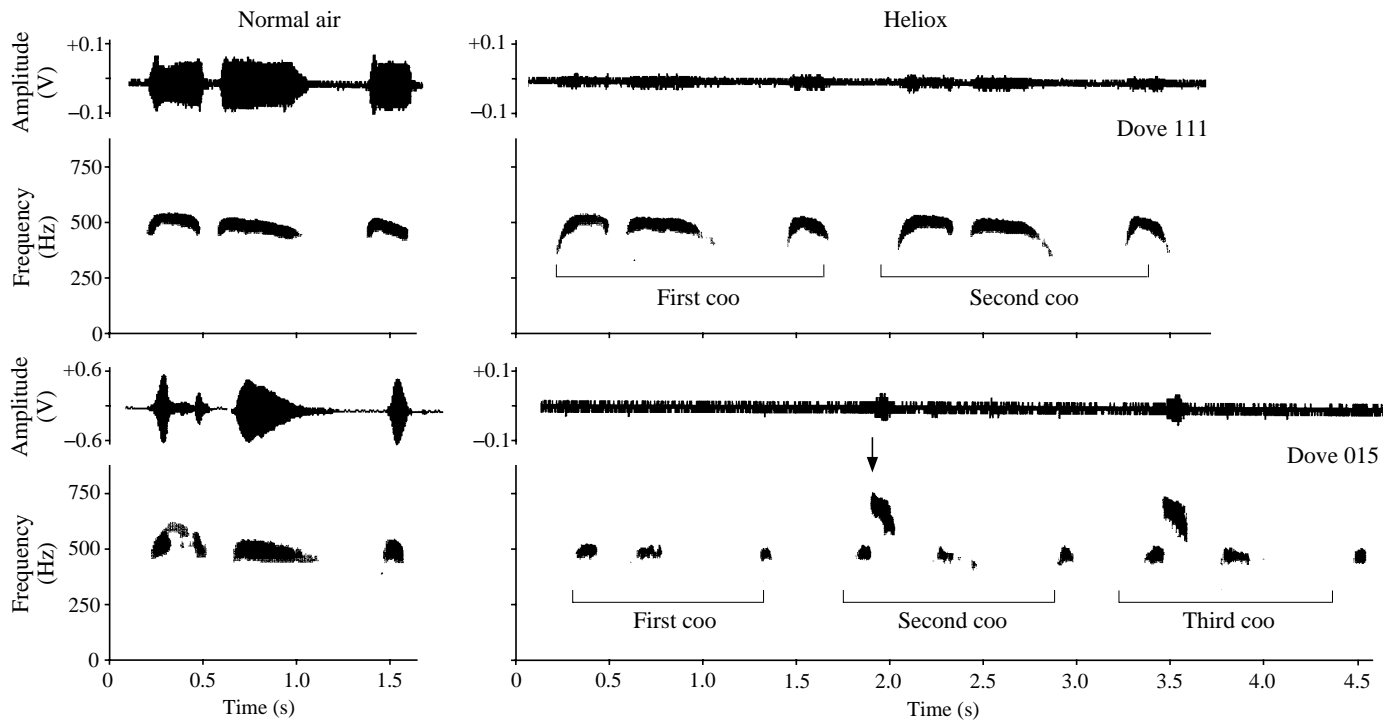


Fig. 5. Sonograms and amplitude envelopes of control coos and the first coos produced in heliox (the scale of the amplitude axis varies between normal air and heliox because of the large amplitude difference between the two conditions). Individual 111 produced the first coo bout in heliox 49 min after the start of the pre-experimental period, while individual 015 produced the first coo bout after 28 min. Note that in both individuals the amplitude of the first coo in heliox is extremely low compared with the coo produced in normal air. Furthermore, the first frequency modulation (individual 015, indicated by an arrow) produced in heliox has a much higher frequency than the modulation frequency in normal air.

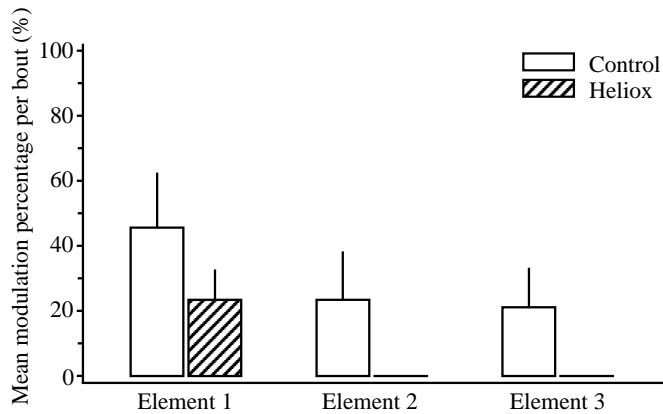


Fig. 6. The effect of heliox on the modulation percentage of the three elements of a coo. Values are means + S.E.M. ($N=4$).

significantly higher than the amplitude of the modulation frequency (individual 015, $t=5.83$, $P<0.001$; individual 178, $t=5.37$, $P<0.001$), in another the reverse was found (individual 160, $t=-2.94$, $P=0.010$), while in individual 008 no significant difference was present (Fig. 7; Table 3). Harmonics, usually twice the modulation frequency, were sometimes present in each of the individuals (Fig. 7; Table 3).

Modulated elements produced in heliox had a completely different structure (Fig. 1, heliox; Fig. 7). In two individuals, the base frequency showed a small significant increase of approximately 3.5% (Fig. 7; Table 3; individual 008, $t=-6.31$, $P<0.001$; individual 015, $t=-3.75$, $P=0.001$). In individual 160, the base frequency decreased significantly by 3.8% ($t=5.14$, $P<0.001$), while individual 178 showed no significant change in base frequency (Fig. 7; Table 3). In all four individuals, the amplitude of the base frequency showed a significant decrease of, on average, 13.2 dB (range -4.9 to -20.6 dB; $t=4.38-8.86$, $P<0.001$; Table 3). The modulation

frequency increased significantly in heliox by approximately 28% (range 23.0–36.4%; $t=-32.56$ to -87.06 , $P<0.001$; Table 3). Interestingly, in all individuals, the modulation frequency was 1.48 ± 0.02 (mean \pm S.D., $N=4$) times the base frequency, irrespective of individual differences in the shift in resonance frequency of the toy flute. In addition, both base and modulation frequency became continuous in time and were visible in the sonogram as two parallel frequency bands (Fig. 1, heliox). The amplitude of the modulation frequency decreased significantly by 18.1 dB (range -10.3 to -25.4 dB; $t=7.82-22.62$, $P<0.001$; Table 3). Furthermore, in two individuals (015 and 178), a low-frequency peak became visible in the power spectrogram, in addition to the base and modulation frequency. This low-frequency peak was, on average, at 242 Hz and in both individuals, exactly half of the base frequency (see Figs 7, 8; Table 3).

The shift in modulation frequency was present in the first modulated elements produced in heliox (Fig. 5). Individual 015 produced its first coo bout in heliox 28 min after the start of the pre-experimental period. The fundamental frequency of the toy flute at that time increased had by more than 40%. The first coo of this particular bout was unmodulated and already showed, as for individual 111, a large decrease in amplitude. The first elements of both the second and third coos of this bout were modulated (Fig. 5). The modulation frequency of the first modulated elements produced in heliox already showed a substantial increase. However, the temporal pattern of these elements still showed some resemblance to that of a modulated element produced in normal air.

Two other individuals provided evidence that the shift in modulation frequency from the pattern in normal air to that in heliox was directly related to the increasing helium concentration in the cage. Individuals 008 and 178 produced several perch-coo bouts during the 15 min pre-experimental period (individual 178 is shown in Fig. 8). During the pre-

Table 3. Frequency and amplitude aspects of modulated elements of perch-coos of collared doves in normal air (A) and heliox (B)

A Control recordings of modulated elements						
Individual	Base frequency (Hz)	Amplitude of base frequency (dB)	Harmonics	Modulation frequency (Hz)	Amplitude of modulation frequency (dB)	Harmonics
008	507 \pm 10	-57.2 \pm 3.2	0	606 \pm 7	-57.1 \pm 2.9	0.6
015	455 \pm 5	-51.1 \pm 2.6	0	517 \pm 10	-58.2 \pm 2.7	0
160	524 \pm 15	-47.0 \pm 4.0	0.4	589 \pm 4	-43.9 \pm 1.7	1.5
178	511 \pm 9	-51.0 \pm 3.9	0	610 \pm 13	-57.6 \pm 3.1	0.8
B Heliox recordings of modulated elements						
Individual	Low-frequency peak (Hz)	Amplitude of low-frequency peak (dB)	Base frequency (Hz)	Amplitude of base frequency (dB)	Modulation frequency (Hz)	Amplitude of modulation frequency (dB)
008	-	-	526 \pm 4	-67.6 \pm 4.7	760 \pm 5	-81.6 \pm 3.2
015	236 \pm 7	-87.9 \pm 1.3	472 \pm 18	-83.6 \pm 4.2	705 \pm 13	-68.7 \pm 2.7
160	-	-	504 \pm 3	-51.9 \pm 1.8	758 \pm 6	-69.3 \pm 4.4
178	249 \pm 4	-82.7 \pm 2.7	505 \pm 11	-71.6 \pm 9.4	750 \pm 13	-70.0 \pm 6.3

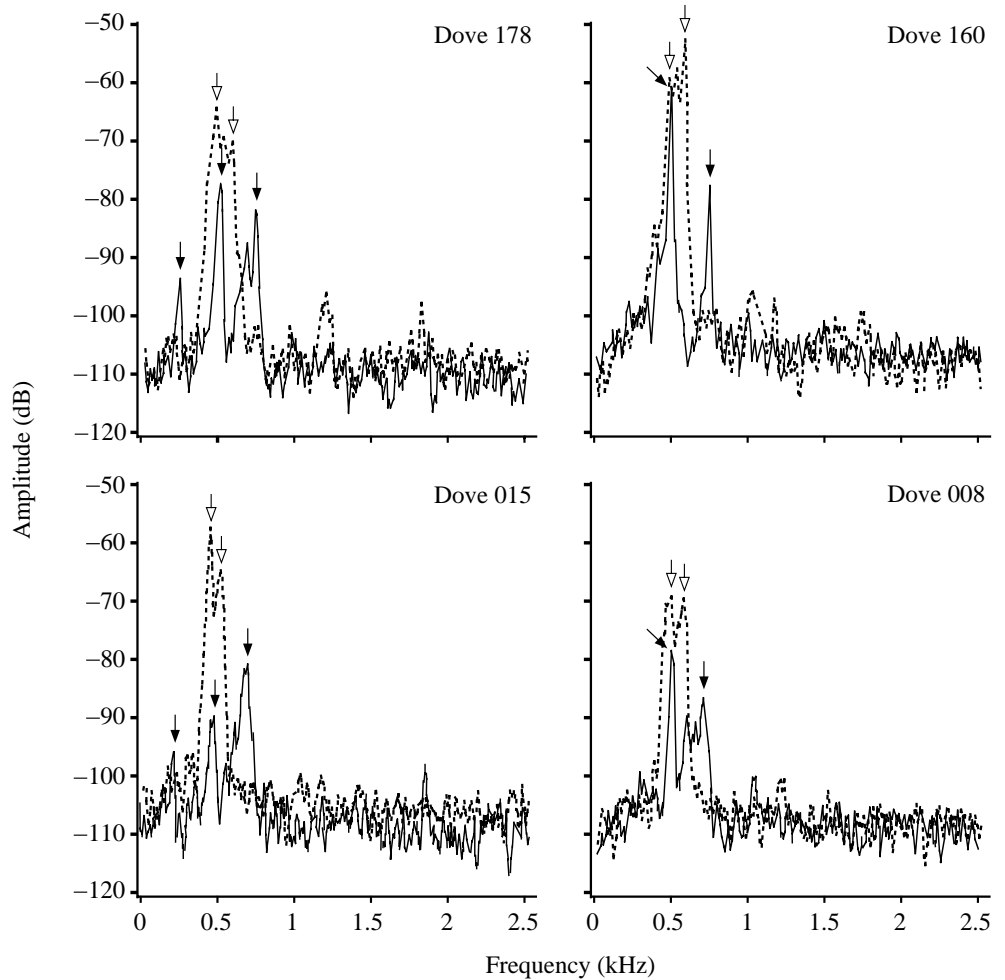


Fig. 7. Power spectra of the modulated elements of perch-coos by four individuals (12.5 kHz sample rate, 2.5 kHz analysis range, 4096 point transforms, 3 Hz frequency resolution). Each power spectrum is a mean calculated over 10–20 modulated elements. Dotted line, normal air; solid line, heliox; open arrows, peak frequencies in normal air; filled arrows, peak frequencies in heliox. Note the presence of a low-frequency peak in heliox for individuals 178 and 015.

experimental period, the effects of heliox increased progressively, thereby increasing the resonance frequency of the toy flute in the experimental cage by approximately 35%. Modulated elements produced early in this period, i.e. during the first 5 min, had a normal spectrotemporal structure (compare Fig. 1, normal air, with Fig. 8). The modulation frequency then increased with increasing helium concentration until it was approximately 1.5 times the base frequency.

Interestingly, when this value of 1.5 times base frequency was reached, the modulation frequency did not increase further, while the resonance frequency of the toy flute continued to increase. Furthermore, the duration of the initial part of the unmodulated element increased, giving a continuous trace throughout the entire element. The low-frequency band of 0.5 times the base frequency became visible after approximately 15 min (Fig. 8).

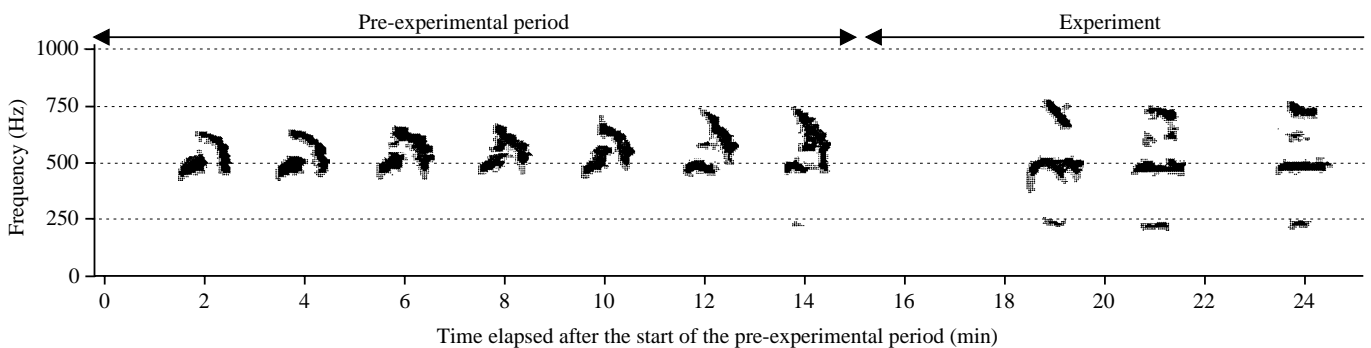


Fig. 8. The gradual change in the spectrotemporal structure of a frequency modulation. Each sonogram is the first element of a coo by dove 178 produced during the pre-experimental period or during the experiment itself.

Discussion

The effects of heliox on the structure of the dove vocalizations differed substantially for unmodulated and modulated elements. Except for a significant decrease in amplitude, unmodulated elements were relatively little affected by the change in atmosphere density. In contrast, both the occurrence and spectrotemporal structure of modulated elements underwent significant changes in heliox. Generally, frequency modulations occurred less often: they were no longer produced in all three elements of a coo, but appeared only in the first. In addition, the modulation frequency showed a gradual increase with increasing helium concentration. The increase in frequency reached a plateau when the modulation frequency was approximately 1.5 times the base frequency, even when the helium concentration continued to increase thereafter. In this period of the experiment, a frequency band at half the base frequency was also sometimes observed.

The discussion will start by focusing on the validity of the 'whistle' model. Next, the role of vocal tract resonances in the production and/or modulation of collared dove vocalizations will be discussed. Lastly, the specific effects of heliox on the structure of frequency modulations will be analyzed.

The validity of the 'whistle' model

The inability of the 'classical' and 'pulse tone' models to explain the production of pure tones (Casey and Gaunt, 1985; Gaunt and Gaunt, 1985), i.e. 'sinusoid-like sounds concentrating acoustic energy at a single frequency' (Nowicki *et al.* 1992), led to the development of an aerodynamic model of sound production: the so-called 'whistle' model (Gaunt *et al.* 1982). In a hole-tone whistle, the type of whistle that would be most appropriate for generating sounds in a bird's syrinx (Gaunt *et al.* 1982), sound is produced when the airflow is forced through a small opening, generating disturbances in the airflow by shearing forces (Chanaud, 1970). Sound that is produced in this manner is typically devoid of harmonics (Casey and Gaunt, 1985).

The 'whistle' model has been derived primarily from anatomical (orange-winged Amazon parrot *Amazonia amazonica*, Nottebohm, 1976; ring dove *Streptopelia decaocto*, Gaunt *et al.* 1982), physiological and acoustic (ring dove, Gaunt *et al.* 1982) data. In general, the syrinx is very similar in parrots and doves (Nottebohm, 1976) and can be characterized by the presence of tracheobronchial junctions which can be easily reduced in diameter by muscle activity and by extensively developed lateral tympaniform membranes (Nottebohm, 1976; Gaunt *et al.* 1982; Ballintijn *et al.* 1995). Gaunt *et al.* (1982) suggested that the tracheobronchial junctions could be narrowed to small slots by activation of the syringeal muscles. When air is forced through these small slots, periodic disturbances in the airflow are created. The in-bulging lateral tympaniform membranes might also cause such constriction (Nottebohm, 1976; Gaunt *et al.* 1982).

One way of gaining insight into how the syrinx might operate is by studying its anatomy. A detailed study of the morphology of the collared dove syrinx suggested that

vocalizations are not produced according to an aerodynamic 'whistle' mechanism, but by the mechanical vibration of the medial tympaniform membranes, which are extremely thin and elastic (Ballintijn *et al.* 1995). Recently, sound production has been studied more directly in the intact syrinx using endoscopic techniques (Goller and Larsen, 1997). Indeed, visualization of the syrinx during air-induced sound generation in deeply anaesthetized pigeons strongly suggested that the lateral tympaniform membranes are the main sound source, being set into vibration by the airflow. Although the in-bulging lateral tympaniform membranes do form some kind of slot, Goller and Larsen (1997) found no evidence that this slot might operate as a 'true' constriction responsible for the generation of series of vortices, as in a whistle.

Another way to study the validity of the 'whistle' model is to record vocalizing birds in a heliox atmosphere. If vocalizations are produced in a similar manner to a whistle, the fundamental frequency of these vocalizations should increase in heliox, because the resonance frequencies of the sound-producing system will be altered by an increase in sound velocity (Hersh, 1967; Gaunt *et al.* 1987; Nowicki, 1987; Nowicki and Marler, 1988; Brittan-Powell *et al.* 1997). The results of the present study are in agreement with studies on songbirds (Nowicki, 1987) and budgerigars *Melopsittacus undulatus* (Brittan-Powell *et al.* 1997). The fundamental frequency of unmodulated elements showed an increase of only a few per cent. This small shift might be explained by minor effects of the decreased air density on the vibrating syringeal membranes (Greenwalt, 1968) and is of a completely different magnitude from the observed shift in the resonance frequency of the toy flute. The absence of a large shift in the fundamental frequency suggests that there is little or no coupling between sound source and resonance frequency (Nowicki, 1987; Nowicki and Marler, 1988; Brittan-Powell *et al.* 1997). Therefore, as suggested previously (Ballintijn *et al.* 1995), the vocalizations of the collared dove are not produced in a manner similar to a whistle. It is more likely that the primary sound source is vibration of the syringeal membranes.

To summarize, the first difficulties for the 'whistle' model arose when Nowicki (1987) showed that the presence of an aerodynamic sound-producing mechanism in songbirds was highly unlikely. Although the 'whistle' model was specifically based on phenomena observed in parrots (Nottebohm, 1976) and doves (Gaunt *et al.* 1982), the recent studies on budgerigars (Brittan-Powell *et al.* 1997) and pigeons *Columba livia* (Goller and Larsen, 1997) and the present study on collared doves do not support it. Nevertheless, in view of the enormous variation in syringeal structure among taxa (King, 1989) and the general lack of knowledge on the fundamental properties of aerodynamic whistles (Nowicki and Marler, 1988), it is still possible that some bird species might produce their vocalizations in a whistle-like manner.

The role of vocal tract resonances

The role of vocal tract resonances in the modulation of bird vocalizations has been studied intensively, and it has been

more or less generally assumed that all modulations are source-generated (reviewed by Gaunt, 1987; Nowicki and Marler, 1988). One of the reasons why Greenwalt (1968) discarded the role of tracheal resonances was the absence of a relationship between the frequency and amplitude of the vocalization and the resonance frequency of the trachea, which can be modelled as a simple tube. Indeed, for many bird species, such as cranes, swans and grouse, no such correlation has been found (summarized by Gaunt, 1987). However, other studies have found evidence that the dominant frequency of bird calls corresponds to the resonance frequency of the trachea (e.g. Brittan-Powell *et al.* 1997).

Collared doves produce coos with a fundamental frequency of approximately 500 Hz (e.g. ten Cate, 1992; Ballintijn and ten Cate, 1997*a,b*). Although dove vocalizations are almost pure tones, their power spectra sometimes reveal weak harmonics, both even and odd, suggesting that the trachea acts as a tube open or closed at both ends. If this is so, harmonic frequencies are determined by the following equation: $F_n = (nV)/2L$, where F is frequency, n is the number of the harmonic, V is the velocity of sound in normal air and L is the length of the trachea. According to this equation, to produce a dominant frequency at 500 Hz (first harmonic), the trachea would have to measure approximately 33 cm. The actual length of the collared dove trachea is much less, on average 7.7 cm (Ballintijn and ten Cate, 1997*a*), which would correspond to a resonance frequency of 2150 Hz. However, the trachea is not the only part of the vocal tract in doves. During cooing, a dove keeps its bill and nostrils closed, while the airflow from the trachea is diverted into the oesophagus and crop (Gaunt *et al.* 1982). Gaunt and Wells (1973) suggested that the oesophagus and its related airsacs might contribute to sound production directly or through some sort of resonance phenomenon. If the oesophagus is considered as part of the vocal tract, the assumed tube length of 7.7 cm will underestimate the actual length of the vocal tract. However, the lack of a change in frequency when the oesophageal chamber expands has led to the suggestion that the resonant properties of the oesophagus are not involved in determining the frequency of the coo (Gaunt *et al.* 1982). Overall, there is no clear correlation between resonance and dominant frequency in the collared dove.

Nowicki (1987) suggested that resonances, which are determined by the size, shape and elasticity of the resonant cavity, might act as an acoustic filter, which selectively enhances or dampens certain frequencies in the vocalizations. This way, pure tones might be produced as harmonic sounds at the syrinx and the harmonic context would be filtered when the sound passed through the vocal tract. The properties of this acoustic filter are determined by the resonance frequencies of the vocal tract. In normal air, the filter is centred around the dominant frequency, but when air is replaced with a mixture of a lower density, such as heliox, the filter would shift upwards as resonance frequencies are altered. Such a shift would result in a reduction in the amplitude of the dominant frequency, which would be dampened to a certain degree (Nowicki, 1987; Nowicki and Marler, 1988). Although

previous studies failed to show a significant decrease in the amplitude of the fundamental frequency in heliox (Hersh, 1967; Gaunt *et al.* 1987; Brittan-Powell *et al.* 1997), such a significant decrease was found in the present study. Theoretically, depending on the harmonic structure produced at the syrinx, an increase in the amplitude of the second or third harmonic might also be measurable, as these frequencies are enhanced by the shifted resonances of the vocal tract (Nowicki and Marler, 1988). In line with this theory, budgerigar calls produced in heliox showed an overall increase in the energy content of frequencies above the fundamental frequency (Brittan-Powell *et al.* 1997). However, in the present study, the amplitude of the harmonics of the coos in the collared dove appeared to decrease, resulting in an overall decrease in the number of harmonics. Furthermore, when measuring the mean amplitude in a 100 Hz frequency band around the hypothetically shifted fundamental frequency, a significant decrease, instead of an increase, in amplitude was found.

To summarize, vocal tract resonances enhance the fundamental frequency of the collared dove coo, even though the resonance frequency of the trachea is of a completely different order. However, no evidence was found to support the presence of a vocal filter, as has been suggested by Nowicki and Marler (1988). Without further study, it may be assumed that the almost pure tonal vocalizations are actually produced as such in the syrinx and undergo limited modification of their frequency profile when passing through the vocal tract.

Effect of heliox on frequency modulations

The present study revealed that altering the density of the atmosphere in which vocalizations are produced had a pronounced effect on both the occurrence and spectrotemporal structure of frequency modulations. The overall occurrence of frequency modulations decreased in four out of five individuals, and frequency modulations were only produced on the first element. In addition, the spectrotemporal structure revealed three major changes: (1) a helium-concentration-dependent increase in modulation frequency from approximately 1.16 times the base frequency in normal air to 1.48 times the base frequency in heliox, above which there was no further increase with increasing helium concentration, (2) the base and modulation frequencies became two parallel frequency bands in the sonogram, while in normal air there was little overlap on the time axis, and (3) a new frequency band became visible at half the base frequency in half of the individuals. Therefore, in general, the original frequency modulation changed into a harmonic series of frequency bands with the base frequency becoming the second harmonic.

A possible explanation for the increase in bout length, the decrease in the occurrence of frequency modulations and the changed spectrotemporal structure of modulated elements in heliox may be that the doves become 'aware' of the change in atmosphere as a result of acoustic feedback mechanisms. It is possible that the doves alter their acoustic behaviour in heliox by reducing their effort and preferentially producing unmodulated elements only. The decrease in amplitude may be

the result of a decrease in effort by the doves, whilst the increase in bout length may be seen as a way of 'exploring' the acoustic effects of the changed atmosphere. This hypothesis would also imply that the modulated elements in heliox are in fact unmodulated elements. The fundamental frequency of these 'unmodulated' elements, approximately 250 Hz, might be suppressed in normal air, while in heliox the first, second and third harmonics become visible. It is also possible that, in heliox, sidebands around the fundamental frequency of approximately 500 Hz are seen. Although this hypothesis partly explains the results, there is strong evidence against treating the changes in spectrotemporal structure of heliox-produced elements as the result of behavioural adaptation.

The 'behavioural adaptation' hypothesis requires that doves first receive acoustic feedback in the altered atmosphere, after which they may alter their acoustic behaviour. This implies that any changes in the first coos produced in heliox will not be the result of a change in behaviour. The present study showed that the first coos produced in the helium atmosphere already had a lower amplitude. In addition, when the first coo bout produced in heliox contained modulated elements, these modulated elements already had an altered spectral structure. As these amplitude and spectral changes occur in the first coos produced in heliox, they cannot have been the result of a behavioural adaptation to the changed atmosphere. Furthermore, if doves preferentially produce unmodulated elements in heliox, it is unclear why all unmodulated elements do not have the same spectrotemporal structure. The two different categories of spectrotemporal profile, i.e. elements with and without the frequency bands at 250 and 750 Hz, indicate that two different types of elements are being produced in heliox. Although the influence of acoustic feedback on acoustic behaviour could only be excluded if the dove was deafened in heliox, it may be assumed that the changes in the spectrotemporal structure of the collared dove coos in the present study are mainly an effect of the change in atmosphere and thus a change in the resonance properties of the sound-producing mechanism.

The production of frequency modulations in the collared dove is still poorly understood. Abs (1980) showed, using artificial membranes, that a gradual rise in the speed of the airflow along a vibrating membrane may lead to an abrupt change in frequency when a certain threshold in air speed was crossed. On the basis of this study, ten Cate (1992) suggested that a similar mechanism might be responsible for the production of frequency modulations in collared doves, i.e. both unmodulated and modulated elements are produced by membrane vibrations, with the latter being produced at a higher air speed. If so, the modulation frequency, as for the frequency of unmodulated elements, should be unaffected by the heliox. The present study showed clearly that this is not the case, suggesting a possible differentiation in sound-producing mechanisms for unmodulated and modulated elements.

An individual may use different sound-producing mechanisms to produce different types of vocalizations (Klatt

and Stefanski, 1974; Gaunt and Gaunt, 1977; Brackenbury, 1989), as in many corvids, psittacids, mimids and sturnids (Gaunt, 1987). The present study showed that, although the base frequency was unaffected, the modulation frequency increased significantly in heliox. Furthermore, the increase in modulation frequency appeared to be coupled to the helium concentration in the experimental cage. A gradual increase in helium concentration resulted in a gradual increase in modulation frequency. This suggests that the modulation frequency, and to a lesser extent the base frequency, may be determined or modulated by the resonance characteristics of the vocal tract.

There are at least two possible underlying mechanisms that could create such a result. The first is that the modulation frequency is produced by a vibrating membrane which is strongly coupled to a resonator, as in a musical wind instrument (Nowicki and Marler, 1988). It is possible that the medial tympaniform membranes are involved in the process of creating resonances. The morphological structure of these membranes, i.e. thin and elastic, makes them highly vibratile (Ballintijn *et al.* 1995). Furthermore, Goller and Larsen (1997) showed that, although the medial tympaniform membranes are not essential to sound production, they have a strong modulatory effect on the spectrographic structure of a vocalization. Interestingly, the main effect of disabling the medial tympaniform membranes using tissue adhesive, i.e. a shift of energy from the second harmonic to the first harmonic (Goller and Larsen, 1997), is very similar to the effect of heliox in causing the appearance of a low-frequency band observed in the present study. The second possible mechanism is that the modulation frequency is produced by a whistle-like mechanism. It is known that some whistles tend to show an abrupt change in frequency when a certain threshold in the speed of the airflow is reached (Chanaud, 1970; Wilson *et al.* 1971). From the results of the present study, it is not possible to distinguish between these two mechanisms, since changing the resonance frequency by replacing normal air with heliox would result in a concentration-dependent effect on the modulation frequency in both cases. Nevertheless, it is clear that vocal tract resonances play an important role in the production of frequency modulations in the collared dove.

Different mechanisms for the production of unmodulated and modulated elements, irrespective of their exact nature, might be a possible explanation for the increase in modulation frequency in heliox, but this does not explain why the spectrotemporal structure of the modulated element changes to a harmonic series with a fundamental frequency of half the base frequency. The change from a pure tonal vocalization to a harmonic vocalization might indicate that a different sound-producing mechanism for modulated sounds is operating in heliox. However, the precise sound-producing mechanism of the frequency modulations will have to be unravelled by more direct physiological studies measuring airflow, air pressure, membrane movements and muscle activity within the syrinx.

Although we cannot, as yet, derive a clear explanation for the phenomenon, our study is the first to obtain clear shifts in

the frequency of vocalizations in heliox, indicating a significant role for vocal tract resonances in the sound-producing process.

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