Vocal tract modelling in fallow deer: are male groans nasalized?

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15

16 **ABSTRACT**

17 Males of several species of deer have a descended and mobile larynx,

18 resulting in an unusually long vocal tract, which can be further extended by

19 lowering the larynx during call production. Formant frequencies are lowered

20 as the vocal tract is extended, as predicted when approximating the vocal

21 tract as a uniform quarter wavelength resonator. However, formant

22 frequencies in polygynous deer follow uneven distribution patterns, indicating

23 that the vocal tract configuration may in fact be rather complex. We CT-

24 scanned the head and neck region of two adult male fallow deer specimens

25 with artificially extended vocal tracts and measured the cross-sectional areas

26 of the supra-laryngeal vocal tract along the oral and nasal tracts. The CT data

27 was then used to predict the resonances produced by three possible

28 configurations, including the oral vocal tract only, the nasal vocal tract only, or

29 combining both. We found that the area functions from the combined oral and

30 nasal vocal tracts produced resonances more closely matching the formant

31 pattern and scaling observed in fallow deer groans than those predicted by

32 the area functions of the oral vocal tract only or of the nasal vocal tract only.

33 This indicates that the nasal and oral vocal tracts are both simultaneously

34 involved in the production of a nonhuman mammal vocalisation, and suggests

35 that the potential for nasalization in putative oral loud-calls should be carefully

36 considered.

37

INTRODUCTION

A key objective of mammal vocal communication research is to determine whether the acoustic structure of vocal signals encodes functionally relevant information. To achieve this aim in a given species it is important to understand how vocal signals are produced because any potential acoustic variation is primarily constrained by the biomechanical properties and dimensions of the caller's vocal anatomy (Fitch and Hauser, 2002). While the causal links between vocal production and acoustic variation are well established in human speech (Titze, 1989; Titze, 1994), the biomechanical and physiological sources of acoustic diversity in nonhuman animal signals remain poorly understood. Nonetheless, the generalization of the source-filter theory of human voice production (Fant, 1960) to non-human mammal vocal signals has significantly advanced our understanding of the acoustic structure of mammalian calls in light of their production mechanisms (reviewed by Taylor et al., 2016). According to this theory, voiced vocalizations are the result of a two-stage production process. First, the source signal is generated in the larynx by vocal fold vibration. The rate at which the glottis opens and closes determines the fundamental frequency (F0) of the vocalisation (the main perceptual correlate of the pitch). The source signal is subsequently filtered by the supra-laryngeal vocal tract, whose resonance frequencies shape the spectral envelope of the radiated vocalization, creating broad bands of energy called 'formants' (Fitch, 2000a). Because F0 and formants are produced independently they are subject to separate biomechanical constraints.

Recent anatomical investigations of mammal supra-laryngeal vocal tracts have revealed an extensive diversity of vocal tract morphology, with e.g., elongated noses (Frey et al., 2007b), air sacs (Frey et al., 2007a) and descended larynges (Frey and Gebler, 2003), suggesting that vocal tract resonances are under strong selection pressures. Yet, to conclusively determine how such anatomical specialisations affect vocal production requires three-dimensional cineradiography to visualise call-synchronous internal dynamic changes in vocal tract shape and document the position of

72   oscillating structures during call production (Fitch, 2000b). This approach is
73   however logistically difficult - if not impossible - to perform on large wild
74   animals. An alternative method is to obtain precise vocal tract geometries
75   from cadavers and use this data to generate vocal tract geometries that
76   provide predictions of formant values for multiple vocal tract configurations.
77   Several studies of nonhuman mammals have used this approach to predict
78   the resonance characteristics of air spaces in the upper respiratory tract,
79   showing good concordance with actual formant patterns in species-specific
80   vocalisations (Adam et al., 2013; Carterette et al.,1979, 1984; Gamba et al.,
81   2012; Gamba and Giacoma, 2006b; Koda et al., 2012; Riede et al., 2005).
82   Studies investigating the evolutionary origins of speech have also used vocal
83   tract models to predict the potential articulatory abilities of human ancestors
84   (Boë et al., 2002; Lieberman et al., 1972) as well as non-human primates
85   (Boë et al., 2002; Boë et al., 2017; Fitch et al., 2016). However, attempts at
86   predicting vocal tract resonances from anatomical data remain scant and
87   largely focused on primate species (Gamba et al., 2012; Gamba and
88   Giacoma, 2006a; Koda et al., 2012; Riede et al., 2005), essentially due to the
89   lack of data on vocal tract geometries available for nonhuman terrestrial
90   mammals.

91

92   During the autumn breeding season, male fallow deer (*Dama dama*) produce
93   high rates of sexually selected groan vocalisations (Briefer et al., 2010;
94   McElligott and Hayden, 1999). Groans are characterized by a very low F0
95   and unevenly spaced and modulated formants that obey stereotyped
96   distribution patterns, indicating that they are produced by a consistent, but
97   complex vocal tract shape (Reby et al., 1998; Vannoni and McElligott, 2007).
98   Fallow bucks have a descended and mobile larynx that is retracted towards
99   the sternum during groan production (Fitch and Reby, 2001; McElligott et al.,
100   2006), thereby extending the vocal tract. The effect of vocal tract extension on
101   formant frequencies has been extensively documented in fallow deer
102   (McElligott et al., 2006) and the closely related red deer (Fitch and Reby,
103   2001; Frey et al., 2012). As the animal extends its vocal tract, formants are
104   lowered until they reach a minimal plateau corresponding to maximal
105   extension, and formant frequency spacing is inversely correlated with the

106 length of the vocal tract during extension (Fitch and Reby, 2001; McElligott et
107 al., 2006).

108

109 Previous attempts at relating formant frequency spacing to vocal tract length
110 have typically modelled the vocal tract as a simple tube of uniform diameter
111 that is closed at the glottis and opened at the mouth (Charlton et al., 2011;
112 Reby and McComb, 2003; Vannoni and McElligott, 2007; Fitch, 1997). Under
113 these assumptions, the length of the vocal tract can be predicted from the
114 formant frequency spacing (and vice-versa) using the equation: eVTL =
115 c/2*DF, where eVTL = estimated vocal tract length, c = the speed of sound in
116 the vocal tract of 350 m/s, and DF is the overall formant frequency spacing
117 measured in the vocalization (Reby and McComb, 2003). Measurements of
118 anatomical oral vocal tract length in adult male fallow deer (taken as the
119 distance from the larynx to the tip of the snout) based on calibrated
120 photographs have produced fully extended vocal tract lengths ranging
121 between 46 cm and 54 cm (McElligott et al., 2006). Yet, the minimum formant
122 spacing (DF) measured in male fallow deer groans varies between 326 Hz to
123 281 Hz (Vannoni and McElligott, 2007), which, when the vocal tract is
124 modelled as a simple cylindrical tube, corresponds to vocal tract lengths
125 between 54 cm and 62 cm. This overestimation of the vocal tract length from
126 the acoustic data indicates that the animal's vocal tract produces more/lower
127 formants than expected from its anatomical length. Combined with the
128 observation that formants are stereotypically unevenly spaced in groans
129 (McElligott et al., 2006), this suggests the vocal tract configuration during
130 groan production is more complex than previously assumed.

131

132 Here we investigate the hypothesis that male fallow deer simultaneously use
133 the oral and nasal vocal tracts as resonating systems during call production,
134 allowing this species to produce a larger number of formants and a more
135 complex formant pattern than predicted by a simple cylindrical tube model. To
136 this end, we performed computed tomography (CT) scans of head-and-neck
137 specimens of male fallow deer to achieve a more detailed description of the
138 complex anatomical structure of the male fallow deer supra-laryngeal vocal
139 tract. The specific aims of this investigation are threefold: 1) to describe the 3-

140   dimensional geometry of the supra-laryngeal vocal tract in male fallow deer,
141   including the oral and nasal vocal tracts, while the larynx is maximally
142   retracted; 2) to predict the resonance patterns produced by the fully extended
143   vocal tract configuration, simulating the effect of the involvement of the oral
144   vocal tract only, of the nasal vocal tract only, or of the combined oral and
145   nasal vocal tracts on formant patterns; and 3) to compare resonance patterns
146   predicted by each of these configurations with formant patterns observed in
147   actual vocalisations.
148
149   **MATERIALS AND METHODS**
150
151   A glossary of the anatomical terms used in this article is provided in the
152   appendix and a schematic representation of the mammalian vocal anatomy is
153   provided in the Electronic Supplementary Material.
154
155   **Specimen collection**
156   Our measures of vocal tract area functions are based on CT scans from two
157   adult male fallow deer. Male 1 was a 7-year-old buck that died from injuries
158   sustained during a fight with rival males during the breeding season on Oct
159   20, 2011 in Home Park, London, UK. Male 2 was an 11-year-old buck culled
160   by park staff during annual population control management practices on
161   February 7, 2011 in Richmond Royal Park, London, UK. Both specimens had
162   similar skeletal dimensions: lower mandible length (male 1: 21.0 cm, male 2:
163   20.3 cm) and lower hind leg length from the calcaneal tuber to the end of the
164   metatarsus (male 1: 31 cm, male 2: 32.5 cm). Head-and-neck specimens of
165   both individuals were obtained by separation between the 2nd and 3rd ribs.
166   Specimens were chilled with ice within 2 hours of death and were frozen at -
167   20° C within 5 hours of death.
168
169   **Specimen preparation and CT-Scanning**
170   Specimens were thawed, and water was flushed through the oral and nasal
171   vocal tracts to remove debris and fluids and left upright to drain for about 30
172   minutes before scanning. Specimens were scanned with and without
173   artificially extending the vocal tract. Vocal tract extension was achieved by

174 maximally pulling the sternothyroid muscle and the trachea towards the
175 sternum and fastening them to the sternum using a string. This recreated a
176 naturalistic configuration of the fully extended vocal tract in male fallow deer.
177
178
179 Specimens were positioned as much as possible in configurations typical of
180 vocalising (see figure 1), although it was not possible to stretch the neck as
181 much as desired (figure 2). The oral cavity was kept open using a block of
182 Styrofoam. This affected the position of the tongue which was pushed
183 backward in an unnatural position in one of the specimens. The detrimental
184 effect on the cross-sectional area measures was moderated by extrapolating
185 the typical position of the tongue from other specimens and anatomical
186 examinations.
187
188
189 **Estimation of vocal tract area function**
190 We measured the supra-laryngeal vocal tract area functions (the cross-
191 sectional area at 1 cm steps along the length of the vocal tract, DeBoer and
192 Fitch 2009) using the 3D curved Multi-Planar Representation viewer in Osirix
193 (version 6.0, 64bits for Mac, www.osirix-viewer.com) and following the three-
194 step method described in Kim et al. (2009). First, the oral and nasal vocal
195 tract dorso-ventral midlines were drawn manually using the "3D curved path"
196 tool on a midsagittal section (figure 3). Second, for each vocal tract, cross-
197 sectional areas orthogonal to the midline were produced at 1 cm intervals
198 from the glottis to the lips or nostrils (figure 3). The vocal tract area was then
199 measured in each cross-sectional slice using the closed polygon selection tool
200 to delineate the VT area. Osirix automatically returned the area of the
201 delineated zone (in cm^2). Each slice/measure was saved as an image file.
202
203
204 **Prediction of vocal tract resonances**
205 The position and amplitude of vocal tract resonances were predicted using the
206 transfer matrix method (Chaigne and Kergomard, 2016), where the tube
207 geometry is approximated as a series of cylindrical elements with variable

208   cross sections and 1 cm in length. The transfer matrix model is commonly
209   used for modelling acoustic propagation in tube lattices. The method is
210   appropriate when one dimension of the tube is substantially larger than the
211   others, as in most mammalian vocal tracts: below a cut-off frequency F_{co},
212   ($F_{co} \approx \frac{c}{2D}$, where c is the speed of sound and D the largest transverse
213   dimension) it can be assumed that only plane waves propagate. In this study
214   F_{co} is 4000 Hz as D remains below 4 cm in the fallow deer vocal tract.
215   Assuming linear propagation, the internal acoustic field is perfectly defined by
216   scalar quantities in the frequency domain: the complex amplitudes of the
217   acoustic pressure P and that of the acoustic volume velocity U. For a given
218   cylindrical tube portion of length L and cross sectional area A_o, a 2x2 matrix of
219   complex elements relates vectors {P, U} on both sides (input, output) of the
220   cylinder:

221
$$\begin{pmatrix} P_{in} \\ U_{in} \end{pmatrix} = \begin{pmatrix} \cos kL & i\,Z_c \sin kL \\ i\,Z_c^{-1} \sin kL & \cos kL \end{pmatrix} \begin{pmatrix} P_{out} \\ U_{out} \end{pmatrix},$$

222   where $Z_c = \dfrac{\rho\,c}{A_o}$ is the characteristic impedance (where ρ and c are

223   respectively the air density and the speed of sound at body temperature, and

224    $k = \dfrac{\omega}{c} = \dfrac{2\pi F}{c}$ is the wave number).

225   For complex cylindrical geometry, the tube is broken down into smaller
226   elementary cylindrical tubes. If the tube is described by N elementary
227   cylindrical tubes, acoustic pressure and volume flow at the input and output of
228   the tube are related by the matrix equal to the product of the N matrices of the
229   elementary cells:

230
$$\begin{pmatrix} P_{in} \\ U_{in} \end{pmatrix} = \begin{pmatrix} A & B \\ C & D \end{pmatrix} \begin{pmatrix} P_{out} \\ U_{out} \end{pmatrix}$$

231   It is thus possible to calculate the input impedance Z_{in}:

232
$$Z_{in} = \frac{P_{in}}{U_{in}} = \frac{A\,P_{out} + B\,U_{out}}{C\,P_{out} + D\,U_{out}} = \frac{A\,Z_{out} + B}{C\,Z_{out} + D},$$

233   where $Z_{out} = \dfrac{P_{out}}{U_{out}}$ is the terminal impedance of the tube. If the tube is open (at

234   the mouth and nostrils for example), Z_{out} is the radiation impedance.

235 If several complex tubes are connected (for example at the branching point of

236 the oral and nasal tracts), there is continuity of the acoustic pressure and

237 conservation of the acoustic volume flow. The particular frequencies where

238 the input impedance magnitude reaches a local maximum, correspond to the

239 vocal tract resonances visible as formants in the spectral acoustic structure of

240 the produced vocalisation.

241 The input parameters are the area functions of the oral and nasal vocal tracts

242 and the branching point of the tracts. The air temperature inside the fallow

243 deer vocal tract, which affects the absolute frequency of predicted resonances

244 (formant frequencies are proportional to the speed of sound in the air and thus

245 to the square root of the absolute temperature) but not their relative frequency

246 distribution, was set to 38°C. The model assumed wall damping of rigid walls

247 and radiation impedance of an open end, un-flanged tube (Chaigne and

248 Kergomard, 2016).

249

250 Resonances were predicted for each male, based on the area functions of

251 three possible configurations:

252 (1) the oral vocal tract only (common laryngopharyngeal tract, oropharynx and

253 oral cavity),

254 (2) the nasal vocal tract only (common laryngopharyngeal tract, nasopharynx

255 and nasal cavities),

256 (3) both the oral and nasal vocal tracts (common laryngopharyngeal tract,

257 oropharynx, oral cavity, nasopharynx, nasal cavities).

258

259 The total cross-sectional areas of both (left and right) nasal cavities were

260 approximated by doubling the cross-sectional areas measured for the left

261 nasal cavity connecting to the left nostril. To approximate the potential effect

262 of the partial opening of the sides of the mouth, we only included half of the

263 portion of the oral cavity that is laterally open. The cross-sectional areas for

264 this portion of the oral cavity were estimated by manually linking the upper lip

265 to the lower lip.

266

267

268 **RESULTS**

269   **Vocal tract anatomy**

270   The potential complete vocal tract is composed of five distinct and connected
271   sections, one of which is paired: 1) the common laryngopharyngeal tract,
272   shared by the oral and nasal vocal tract, between the glottis and the intra-
273   pharyngeal ostium, 2) the oropharynx, from the intra-pharyngeal ostium to the
274   Isthmus faucium (oropharyngeal tract), 3) the oral cavity, from the Isthmus
275   faucium to the mouth opening (oral tract), 4) the nasopharynx, from the intra-
276   pharyngeal ostium to the choanae (nasopharyngeal tract), 5) the paired nasal
277   cavities, from the choanae to the nostrils (nasal tract). The oral vocal tract
278   comprises parts 1,2,3 and the nasal vocal tract parts 1,4,5 (figure 2). The
279   choanae and the Isthmus faucium are located approximately at the same
280   distance from the glottis.

281

282   In the resting configuration (figures 1A, 2A and 4A, B), the pharynx, soft
283   palate and thyrohyoid ligament are relaxed, and the larynx resides at the level
284   of cervical vertebrae 2 and 3, however farther rostrally in male 2 than in male
285   1. Accordingly, the rostral end of the trachea is located 41 cm from the lips in
286   male 1 and 34 cm in male 2. The resting oral vocal tract lengths (glottis to lips)
287   are 36 cm in male 1 and 30 cm in male 2, and the resting nasal vocal tract
288   lengths (glottis to nostrils) are 40 cm in male 1 and 35 cm in male 2 (figures
289   4A, B and 5). The flexible region between the rostral edge of the thyroid
290   cartilage and the base of the epiglottis is relaxed and short (4 cm in both male
291   1 and male 2). Correspondingly, the overall length of the larynx (from cricoid
292   arch to epiglottal tip) is 13 cm in male 1 and 10 cm in male 2. The hyoid
293   apparatus is folded and the distance between the basihyoid and the epiglottis
294   is small (4.5 cm in male 1 and 2.5 cm in male 2). The rostral edge of the intra-
295   pharyngeal ostium (the caudal tip of the palatine velum) is located about 30
296   cm from the lips in male 1 and 25 cm in male 2. The epiglottis is in contact
297   with the intra-pharyngeal ostium or overlaps its rostral edge, so that the
298   laryngeal entrance comes to lie in continuation of the nasopharynx (so-called
299   'intranarial position'). The mouth is mostly closed.

300

301   In the extended phonatory configuration (figures 1B, 2B, 3A, 3D and 4C, D),
302   the pharynx, soft palate and thyrohyoid ligament are maximally extended, and

303 the larynx resides at the level of cervical vertebrae 4, 5 and 6 in male 1 and 3,

304 4 and 5 in male 2. Accordingly, the rostral end of the trachea is located

305 approximately 54 cm from the lips in male 1 and 44 cm in male 2. The

306 extended oral vocal tract lengths (glottis to lips) are 48 cm in male 1 and 40

307 cm in male 2, and the extended nasal vocal tract lengths (glottis to nostrils)

308 are 50 cm in male 1 and 43 cm in male 2 (figures 4C, D and 5). The lengths of

309 the common laryngopharyngeal tract (glottis to intra-pharyngeal ostium) are

310 12 cm and 9 cm for males 1 and 2, respectively (figures 4C, D and 5). The

311 flexible region between the rostral edge of the thyroid cartilage and the base

312 of the epiglottis is maximally tensed and considerably elongated (7.5 cm in

313 male 1 and 5 cm in male 2). Correspondingly, the overall length of the larynx

314 (from cricoid arch to epiglottal tip) is 15 cm in male 1 and 13 cm in male 2.

315 The hyoid apparatus is maximally unfolded and the thyrohyoid rotated

316 caudally. The distance between the basihyoid and the epiglottis has

317 considerably enlarged, being now 12 cm in male 1 and 7.5 cm in male 2. The

318 rostral edge of the intra-pharyngeal ostium (the caudal tip of the palatine

319 velum) is located approximately 37 cm from the lips in male 1 and 31 cm in

320 male 2. The epiglottis is retracted from the intra-pharyngeal ostium so that the

321 laryngeal entrance is in continuation of both the oropharynx and the

322 nasopharynx. From the intra-pharyngeal ostium onward, the pharyngeal cavity

323 splits into two tubes (the nasopharynx connected to the nasal cavities and the

324 oropharynx connected to the oral cavity) completely separated by the soft

325 palate (velum). The mouth is opened for vocalizing.

326

327

328 **Cross-sectional areas**

329 The cross sectional areas measured along each of the male specimen's vocal

330 tracts are shown in figure 5. The area functions from the glottis (right) towards

331 the lips and nostrils (left) are highly comparable between the two specimens.

332 Longitudinally, the choanae and the Isthmus faucium are located about 25-30

333 cm (male 1) and 20-25 cm (male 2) rostral to the glottis, respectively (figure

334 5).

335 The decrease of the cross-sectional area from the glottis towards the intra-

336 pharyngeal ostium is a consequence of the large larynx of male fallow deer.

337 Its considerable dorsoventral height causes a relatively large intra-laryngeal
338 cross-sectional area at the glottis (figure 3D cross-section 1). From the intra-
339 pharyngeal ostium the cross-sectional area of the nasopharynx increases
340 towards the choanae and, similarly, the cross-sectional area of the
341 oropharynx increases towards the Isthmus faucium. Choanae and Isthmus
342 faucium mark the rostral end of the pharynx, i.e. the transition from the
343 nasopharynx to the nasal cavities and from the oropharynx to the oral cavity,
344 respectively. The gradual, mostly uniform increase in cross-sectional area,
345 from the intra-pharyngeal ostium towards the rostral end of the pharynx,
346 reflects the basic funnel-shape of the pharynx, narrowest at its connection to
347 the larynx and widest at its connection to the skull and the oral cavity. From
348 the choanae to the nostrils there is an overall decrease of cross-sectional
349 area as a consequence of the narrowing of the nasal cavities towards the
350 muzzle. The particular decrease of cross-sectional area at around 42 cm in
351 male 1 and at around 37 cm in male 2 comes from the ventral nasal conchae,
352 which narrow the nasal cavities by their extensive, scrolled osseous lamellae
353 (figure 3D cross-section 3). From the Isthmus faucium to the lips the cross-
354 sectional area initially increases and then decreases. In between is a
355 particular decrease at around 39 cm in male 1 and around 33 cm in male 2.
356 The initial increase represents the caudal end of the oral cavity between the
357 Isthmus faucium and the root of the tongue and the final decrease the rostral
358 end of the oral cavity between the lingual fossa and the lips. The intermediate
359 decrease in cross-sectional area results from the lingual torus, an elevation of
360 the tongue in ruminants, which considerably narrows the middle oral cavity.
361 When the mouth is opened and the lower jaw depressed for groan emission
362 the cross-sectional areas of the (then funnel-shaped) oral cavity will increase
363 accordingly in direction towards the lips.
364
365

366 **Predicted Vocal tract resonances**
367 The vocal tract resonances predicted from the vocal tract area functions of
368 male 1 and male 2 and corresponding to the three possible configurations are
369 presented in figure 6. F1 predicted by the combined oral and nasal vocal
370 tracts is in intermediate position between the F1 predicted using the oral vocal

371 tract only, or the nasal vocal tract only. F2 and F3 predicted by the combined
372 oral and nasal vocal tracts corresponds to the F2 predicted by the nasal vocal
373 tract only, and to the F2 predicted by the oral vocal tract only. F4 and F5
374 predicted by the combined oral and nasal vocal tracts corresponds to the F3
375 predicted by the nasal vocal tract only, and to the F3 predicted by the oral
376 vocal tract only (figure 6, table 1).

377

378 The centre frequencies of each predicted formant are reported in table 1. The
379 models using both oral and nasal vocal tracts predict much lower formants
380 overall (average formant spacing of 255 Hz) than models using the oral vocal
381 tract only (average formant spacing of 446 Hz) or models using the nasal
382 vocal tract only (average formant spacing of 358 Hz).

383

384 **Table 1: Predicted centre frequencies for formants F1 to F5 (Hz) and**
385 **estimated formant spacing (DF) for the different vocal tract**
386 **configurations for males 1 and 2.**

configuration	male	F1	F2	F3	F4	F5	DF
oral vocal tract only	1	249	494	1044	1352	1938	410
	2	305	581	1238	1629	2238	482
nasal vocal tract only	1	175	359	771	1166	1534	328
	2	194	505	981	1426	1712	388
combined oral and nasal vocal tracts	1	223	365	495	776	1060	227
	2	255	503	582	992	1302	283

387

388 **Comparison with acoustic observations**
389 Figure 7 plots the average centre frequencies of the first five formants
390 observed in groans from 16 adult fallow deer males (reported in Vannoni and
391 McElligott, 2007, see table 2) against the resonances predicted by our three

392   vocal tract models. The resonances predicted by a vocal tract including both
393   the oral and nasal vocal tracts are a better fit to the observed formants than
394   those predicted by using the oral vocal tract or the nasal vocal tract only: the
395   slope of the regression line is closer to 1 (indicating a better fit of the scaling
396   of the resonances), and R^2 is also higher (indicating a better fit of the pattern
397   of the resonances). Examination of the regression slopes in figure 7 shows
398   that while model 3 (combined oral and nasal vocal tracts) underestimates the
399   formant frequency spacing by 9%, model 1 (oral vocal tract only)
400   overestimates DF by 37% and model 2 (nasal vocal tract only) overestimates
401   DF by 23%. Separate correlations for male 1 and male 2 are given in the
402   Electronic Supplementary Material.

403

404   **Table 2: Average centre frequencies for formants F1 to F5 (Hz) and**
405   **average estimated formant spacing (DF) at maximal vocal tract**
406   **extension from 16 adult males (Vannoni & McElligott 2007).**

Formant:	F1	F2	F3	F4	F5	DF
Average centre frequency (Hz) ± SE	208.5 ±2.0	414.3 ±1.9	575.2 ±3.3	1060.2 ±2.9	1265.9 ±3.2	300.6 ±0.8
Minimum centre frequency (Hz)	152	329	457	966	1170	281
Maximum centre frequency (Hz)	263	496	677	1149	1371	326

407
408

409   **DISCUSSION**

410

411   In this study, the artificially extended vocal apparatuses of two adult male
412   fallow deer were CT-scanned, and the cross-sectional areas of the complete
413   supra-laryngeal vocal tract (common laryngopharyngeal tract, oropharynx,

414 oral cavity, nasopharynx and nasal cavities) of both specimens were
415 measured along the oral and nasal vocal tracts. We then used this data to
416 model resonance patterns produced by these supra-laryngeal cavities
417 including the oral vocal tract only, the nasal vocal tract only or the combined
418 oral and nasal vocal tracts. We found that the configuration combining the oral
419 and nasal vocal tract geometries produced a resonance pattern which more
420 closely matches the formants observed in fallow deer groans, both in term of
421 formant frequency pattern and in term of formant frequency scaling.

422

423 The formants observed in the groans of fallow deer (Briefer et al., 2010;
424 McElligott and Hayden, 1999) and more generally in the sexually-selected
425 calls of male polygynous deer with extensible vocal tracts (Fitch and Reby,
426 2001; Passilongo et al., 2013; Reby and McComb, 2003; Reby et al., 2016)
427 obey stereotyped, uneven formant patterns incompatible with a vocal tract
428 consisting of a simple linear tube. More specifically, in both fallow deer groans
429 (McElligott et al., 2006) and red deer roars (Reby and McComb, 2003) the
430 second and third formants are close to one another and the fourth formant is
431 higher, leaving a gap between the third and fourth formant. Our simulations
432 combining both the oral and nasal vocal tracts predict this pattern.
433 Comparison of the models suggests that formants two and four of fallow deer
434 groans are affiliated to the nasal vocal tract while formants three and five are
435 affiliated to the oral vocal tract.

436

437 In terms of frequency scaling, our predictions resolve the aforementioned
438 mismatch between apparent vocal tract lengths estimated from formant
439 frequencies measured in fallow deer groans and actual anatomical vocal tract
440 length derived from photogrammetric and anatomical data. Presumably this is
441 because the inclusion of formants affiliated to the nasal vocal tract led to an
442 overestimation of apparent vocal tract length in previous studies modelling the
443 fallow deer vocal tract as a single uniform tube. Indeed, previous
444 investigations of apparent vocal tract length (i.e. vocal tract length estimated
445 from formant frequencies) in polygynous deer with descended and mobile
446 larynges (Corsican deer: Kidjo et al., 2008; fallow deer: McElligott et al., 2006;
447 Mesola deer: Passilongo et al., 2013; red deer: Reby and McComb, 2003)

448   have modelled the vocal tract as a linear tube with constant cross-section

449   closed at one end (glottis) and open at the other (mouth), and excluded the

450   involvement of the nasal vocal tract for loud calls produced with an open

451   mouth. While these succeeded at characterizing inter-individual differences in

452   formant frequency spacing (Kidjo et al., 2008; Vannoni and McElligott, 2007),

453   apparent vocal tract length and thus body size (Reby and McComb, 2003;

454   Vannoni and McElligott, 2008), they probably yielded over-estimations of the

455   anatomical vocal tract length.

456

457   The inclusion of nasal resonances in future models should allow for better

458   estimations of apparent vocal tract length from recorded mating calls in these

459   species, thereby potentially enhancing the reliability of bioacoustics tools

460   aimed at assessing body size from vocalisations for research, conservation or

461   wildlife management purposes.

462

463   Taken together our observations strongly suggest that the nasal cavity and

464   oral cavity are both simultaneously involved in the vocal production of fallow

465   deer groans. This involvement of the nasal vocal tract due to the non-closure

466   of the intra-pharyngeal ostium during vocal tract extension maybe widespread

467   in species with a permanently descended larynx and extensible vocal tract

468   (such as other polygynous deer and e.g. goitred gazelles), but also occur in

469   species where callers lower their larynx temporarily for the production of oral

470   (rather than nasal) calls. We suggest that the potential for nasalization of

471   putative oral loud calls should be carefully examined across terrestrial

472   mammals.

473

474   The role of nasal cavities in acoustic output has been investigated in humans

475   using anatomical scans, area functions, vocal tract modeling, and/or acoustic

476   analysis (Dang et al., 1994; Feng and Castelli, 1996; Hattori and Fujimura,

477   1958; Pruthi et al., 2007; Story, 2005). Compared to modulation of the oral

478   vocal tract, nasalization plays a relatively minor role in human speech

479   variation and is often left out of vocal models. However, models that include

480   coupling between the nasal and oral cavity can result in transfer functions that

481   more closely match recorded acoustic output (Dang et al., 1994; Feng and

482 Castelli, 1996). The effects of nasalization are strongest in the lower
483 frequencies (Feng and Castelli, 1996; Pruthi et al., 2007) and include the
484 addition of low frequency formant peaks as observed here in fallow deer
485 groans. Nasal coupling has also been suggested as a likely mechanism for
486 the addition of low spectral peaks in Diana monkey alarm calls (Riede and
487 Zuberbuhler, 2003).

488

489 There are obvious limitations to this investigation. Our dead specimens were
490 scanned in artificial positions constrained by the dimensions of the CT-
491 scanner, and thus only approximate the natural postures of live animals
492 during vocalising. Moreover, the vocal tracts were artificially extended. The
493 geometries are thus approximations of the vocal tract of live animals during
494 vocalizing, and do not account for internal adjustments such as, e.g., the
495 possible contribution of palatopharyngeal muscles. Future investigations could
496 involve performing several scans involving different combinations of varying
497 head/neck angle, extent of the laryngeal descent, or mouth opening; or
498 perform simulations of these parameters (Gamba et al., 2012; Gamba and
499 Giacoma, 2006b). Using a larger sample of specimens would also allow the
500 assessment of inter-individual variation, including the effect of age or size.

501

502 Formants frequencies are known to provide cues to the caller's body size in
503 fallow deer groans and red deer roars, due to a close correlation between
504 formant frequency spacing and body size (McElligott et al., 2006; Reby and
505 McComb, 2003), and are used by male and female receivers to asses rivals
506 and potential mates during the breeding season (Charlton et al., 2008a;
507 Charlton et al., 2007; Charlton et al., 2008b; Pitcher et al., 2015; Reby et al.,
508 2005). The descended larynx and extensible vocal tract of fallow and red deer
509 males (and some other species) are therefore considered to be adaptations
510 that allow callers to maximise the acoustic impression of their body size
511 conveyed to receivers (the "size exaggeration hypothesis" Fitch and Reby,
512 2001; Ohala, 1984). Our investigations show that the involvement of the nasal
513 vocal tract adds additional formants to the lower part of the spectrum, which
514 increases formant density (decreasing formant spacing), and may make the
515 caller sound larger when compared to oral or nasal only calls. Similar

516 functional explanations have been suggested for the evolution of air sacs (de

517 Boer, 2009; Harris et al., 2006), which also increase formant density by

518 adding resonances.

519

520 In conclusion, we contend that, while expensive and technically challenging,

521 using 3-dimensional CT scanning to predict vocal tract resonances can

522 greatly assist the interpretation of formant patterns in mammal vocalizations.

523 We suggest that similar approaches could be generalized to the study of vocal

524 tract resonances in other terrestrial mammals.

525

526

527 **Appendix: Glossary of Anatomical Terms used in this paper (based on**

528 **Constantinescu & Schaller 2012 and own descriptions)**

529

530 **Basihyoid:** unpaired, most ventral, transverse component of hyoid apparatus

531 intercalated between the paired suspension from the skull and the paired

532 arms to the larynx.

533 **Choanae:** the 'internal nares', i.e. the two openings at the caudal end of the

534 nasal cavity, where the paired nasal meatuses lead into the nasopharynx.

535 **Cricoid cartilage:** the most caudal, ring-shaped cartilage of the larynx that is

536 attached to the trachea; it consists of a dorsal plate and a ventral arch.

537 **Epiglottis:** the most rostral cartilage of the larynx; during quiet breathing it

538 has a so-called intranarial position, i.e. it protrudes dorsally, through the intra-

539 pharyngeal ostium, into the nasaopharynx; during an open-mouth call the

540 larynx is withdrawn from the intra-pharyngeal ostium so that it is now

541 positioned in the oropharynx.

542 **Glottis:** forms the vocal source of the larynx; it consists of the two vocal folds,

543 ventral parts of the arytenoid cartilages and the vocal cleft in between the

544 vocal folds; regarding the laryngeal cavity it is positioned between the

545 laryngeal vestibule rostrally, and the infraglottic cavity caudally.

546 **Hyoid apparatus:** a framework of small rod-like bones connecting dorsally to

547 the base of the skull, rostrally to the tongue, and caudally to the larynx; it

548 consists of 3 components: the arms of the paired dorsal part flank the pharynx

549 on both sides and suspend the entire hyoid apparatus from the skull base, it

550 consists of several parts on both sides termed (dorsal to ventral):
551 tympanohyoid, stylohyoid, epihyoid, ceratohyoid; the arms of the paired
552 caudal part connect to the larynx (in fallow deer via the two thyrohyoid
553 ligaments); it consists of one element per side termed thyrohyoid; the
554 unpaired, transverse ventral part connects the two paired structures thereby
555 forming a larger U-shaped fork for suspension from the skull dorsally and a
556 smaller U-shaped fork for connection to the larynx caudally.

557 **Intra-pharyngeal ostium:** opening in the soft palate, creating a passage
558 between nasopharynx and oropharynx; it is bordered by the palatopharyngeal
559 muscle that can constrict the intra-pharyngeal ostium.

560 **Isthmus faucium:** narrow short passage between the mouth cavity and the
561 oropharynx, bounded by the soft palate dorsally, the tongue ventrally, and the
562 palatoglossal arch (a symmetrical, dorsoventral mucosa fold between soft
563 palate and tongue) laterally.

564 **Laryngeal entrance:** rostral entrance to the larynx, bounded by the epiglottis,
565 the aryepiglottic folds and the corniculate processes of the arytenoid
566 cartilages.

567 **Nasopharynx:** nasal part of the pharynx, dorsal to the soft palate; it extends
568 from the choanae to the intrapharyngeal ostium.

569 **Oropharynx**: oral part of the pharynx, ventral to the soft palate; it extends
570 from the isthmus faucium to the base of the epiglottis.

571 **Pharynx**: musculomembraneous cross way of the respiratory and digestive
572 tracts between the oral and nasal cavities rostrally, and the oesophagus and
573 larynx caudally; for the sake of simplicity, and in contrast to textbooks, the
574 pharynx is here not subdivided in 3 parts (nasal, oral and laryngeal) but only
575 in 2 parts (nasal and oral).

576 **Soft palate:** the palatine velum or soft palate, is a soft tissue structure that is
577 laterally fused to the pharyngeal walls; it completely separates naso- and
578 oropharynx, except at the intra-pharyngeal ostium, which represents the only
579 communication between Naso- and Oropharynx; as the pharynx, it extends
580 from the choanae to the larynx.

581 **Thyrohyoid:** paired caudal element of the hyoid apparatus that, together with
582 the basihyoid, forms the smaller U-shaped fork for establishing the connection
583 between the hyoid apparatus and the larynx.

584 **Thyroidhyoid ligament:** replaces the usual thyrohyoid articulation of most
585 mammals by a ligamentous connection between the caudal tip of the
586 thyrohyoid bone (of the hyoid apparatus) and the rostral horn of the thyroid
587 cartilage.
588 **Thyroid cartilage:** The most superficial and largest cartilage of the larynx,
589 unpaired, its two lateral laminae are ventrally fused and enclose most of the
590 laryngeal cavity in between them; its rostral horn connects the larynx to the
591 thyrohyoid of the hyoid apparatus, its caudal horn articulates with the cricoid
592 cartilage in the cricothyroid articulation.
593 **Trachea:** Windpipe, connecting the lungs to the larynx, extends from its
594 bifurcation into the main bronchi caudally to the cricoid cartilage of the larynx
595 rostrally.
596

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602

603 **Competing interests**

604 The authors declare no competing or financial interests.

605

606 **Author contributions**

607 D.R. supervised the research. M.T.W., R.F. and D.R. performed the
608 anatomical and imaging investigations. J.G., J-PD. and D.R. performed the
609 acoustical modelling. D.R., M.T.W., R.F., B.D.C., J-PD. and J.G. wrote the
610 manuscript.

611

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619

Data availability

621 Supporting data and scripts for predicting vocal tract resonances are available
622 on request from the corresponding author.

623

Figure Legends

625

626 **Figure 1. Fallow deer buck in a pre-groaning posture (A) and in a**
627 **groaning posture (B) during the annual rut.** In (A) the neck is not extended,
628 the larynx is in its resting position and the mouth is closed. In (B) the neck is
629 extended, the larynx retracted, and the mouth is opened (no lip rounding).
630 Single frames from a video by D. Belton ©.

631

632 **Figure 2. CT-based 3-D reconstructions of male 1**. (A): larynx and hyoid
633 apparatus in pre-groan (resting) position. (B): larynx and hyoid apparatus in a
634 groaning position at full artificial extension of the vocal tract. The larynx
635 position is shifted caudally by approximately 12 cm. ochre: common
636 laryngopharyngeal tract; green: oropharynx and oral cavity; blue: nasopharynx
637 and nasal cavities.

638

639 **Figure 3. Multi-Planar Representation of a CT scan of male 1 illustrating**
640 **the methodology for measuring the vocal tract area function at maximal**
641 **artificial extension**. (A): manually drawn dorso-ventral and transverse
642 midline through the oral vocal tract; (B): sampling transverse sections along
643 the virtually stretched, un-curved oral vocal tract in 1 cm steps; (C): three
644 examples of the obtained cross-sections highlighting the respective contours
645 of the oral vocal tract in green. (D): Sagittal section of the oral vocal tract (left,
646 midline in red), the nasal vocal tract (right, midline in green) and
647 representative cross-sections at the level of the glottis (1), of the naso- and
648 oro-pharynx separated by the soft palate (2) and of the nasal cavities (3).

649

Figure 4. Midsagittal slices of CT scans of males 1 and 2 with the larynx and vocal tract in a pre-groaning (resting) position (A and B) and in a groaning position with the larynx maximally retracted and the vocal tract fully extended (C and D). C1 – C7, T1 = cervical vertebrae 1-7, first thoracic vertebra; Cart. aryt. = arytenoid cartilage; Cart. cric. = cricoid cartilage; Cart. thyr. = thyroid cartilage; Cav. oris = oral cavity; Choan. = choanae (caudal nasal apertures, internal nares); Epigl. = epiglottis; Glott. = glottis; Ling. = tongue; Nasophar. = nasal part of pharynx; Nostr. = nostrils (rostral nasal apertures, external nares); Orophar. = oral part of pharynx; Ost. intrphar. = intra-pharyngeal ostium (IPO); Palat. dur. = hard palate; Palat. mol. = soft palate ('velum'); Trach. = trachea; o = rostral tip of sternal manubrium; asterisk: position of the basihyoid. Compared to the resting state, the elongation of the oral and nasal vocal tract is 33% in male 1 (A, C) and 25% in male 2 (B, D). Scale: 10 cm

Figure 5. Estimation of oral and nasal vocal tract cross-sectional areas in the maximally extended state, proceeding from right to left, in male 1 (A) and male 2 (B).

Figure 6. **Predicted resonances for the three possible vocal tract configurations of groan production in male 1 (A) and male 2 (B).** Red lines: combined oral and nasal vocal tracts; green lines: nasal vocal tract only; blue lines: oral vocal tract only. The resonance pattern produced by the combined oral and nasal vocal tracts is more similar to the observed formants in fallow deer groans than the resonance patterns of either oral or nasal vocal tract alone.

Figure 7. Correlations between resonances observed in male fallow deer groans (y axis) and resonances predicted from vocal tract geometries of scanned specimens (x axis). Predicted resonances are the average centre frequencies of the first 5 peaks predicted by the cross-sectional areas of the vocal tract of male 1 and 2 including the oral vocal tract only (blue line), the nasal vocal tract only (green line), or both the oral and nasal vocal tracts (red line). The regression slopes inform the fit of the scaling (formant spacing) of

684 the observed resonances to the predicted resonances. The values of R^2

685 provide the fit of the pattern of the observed resonances to the predicted

686 resonances.

687

688

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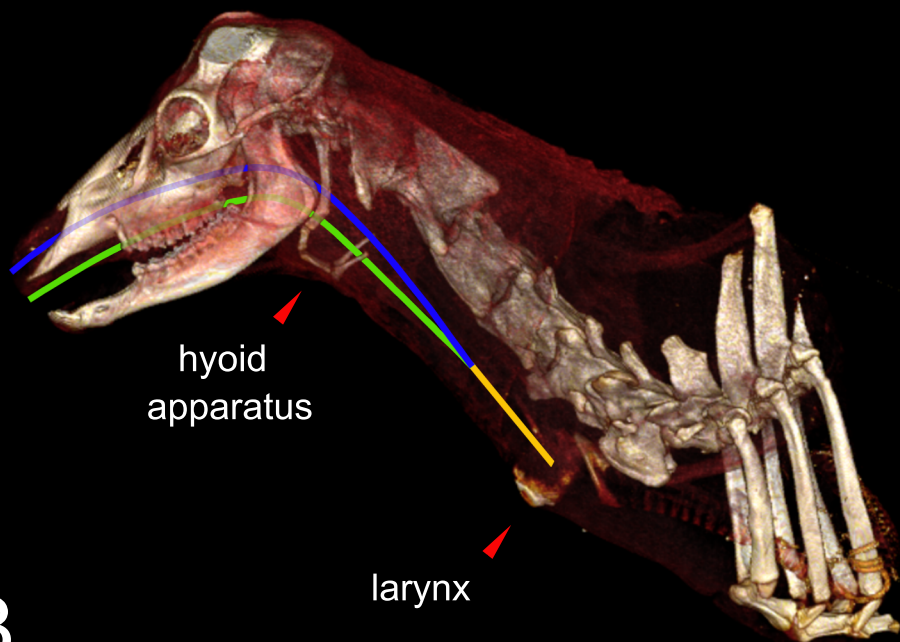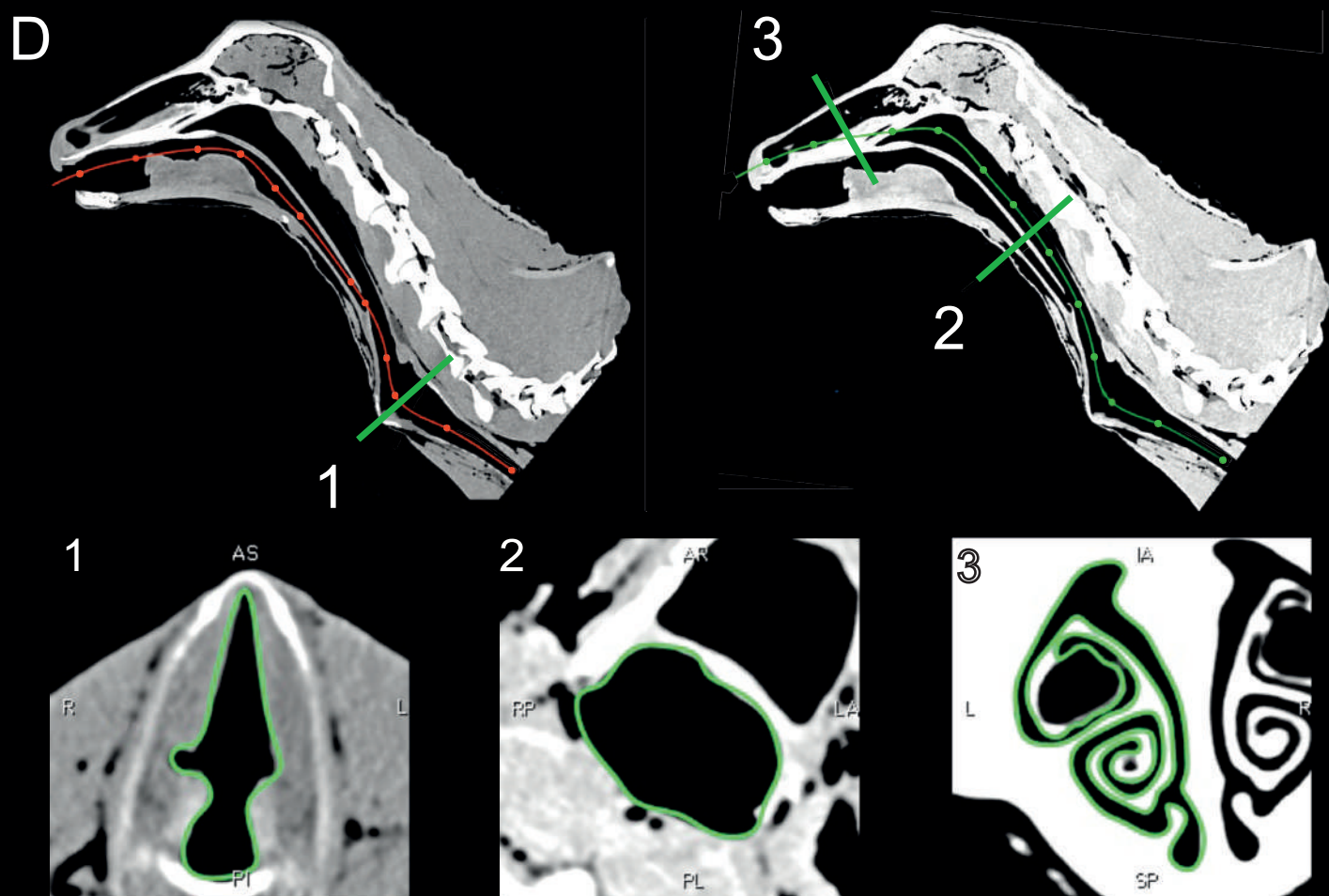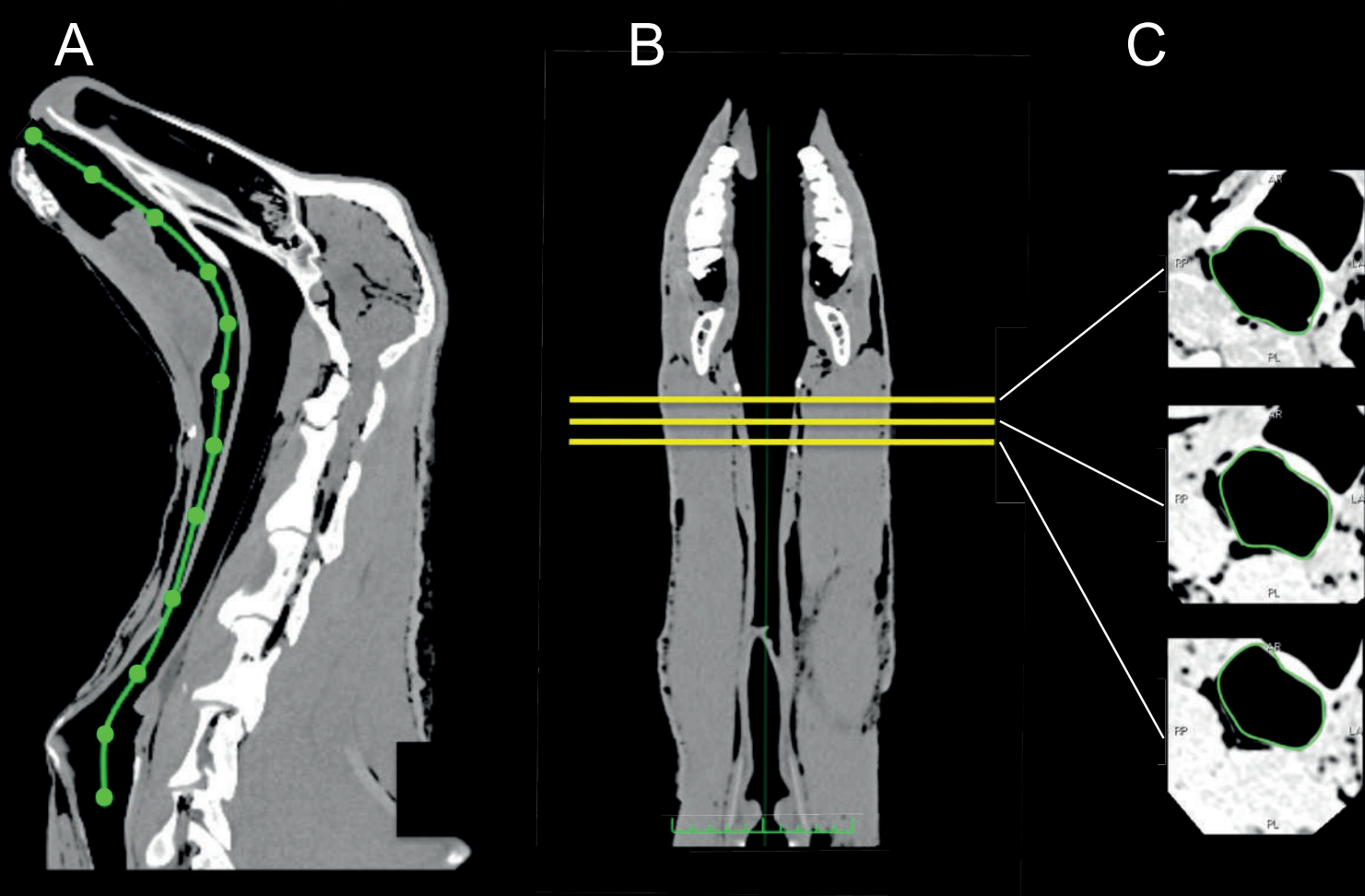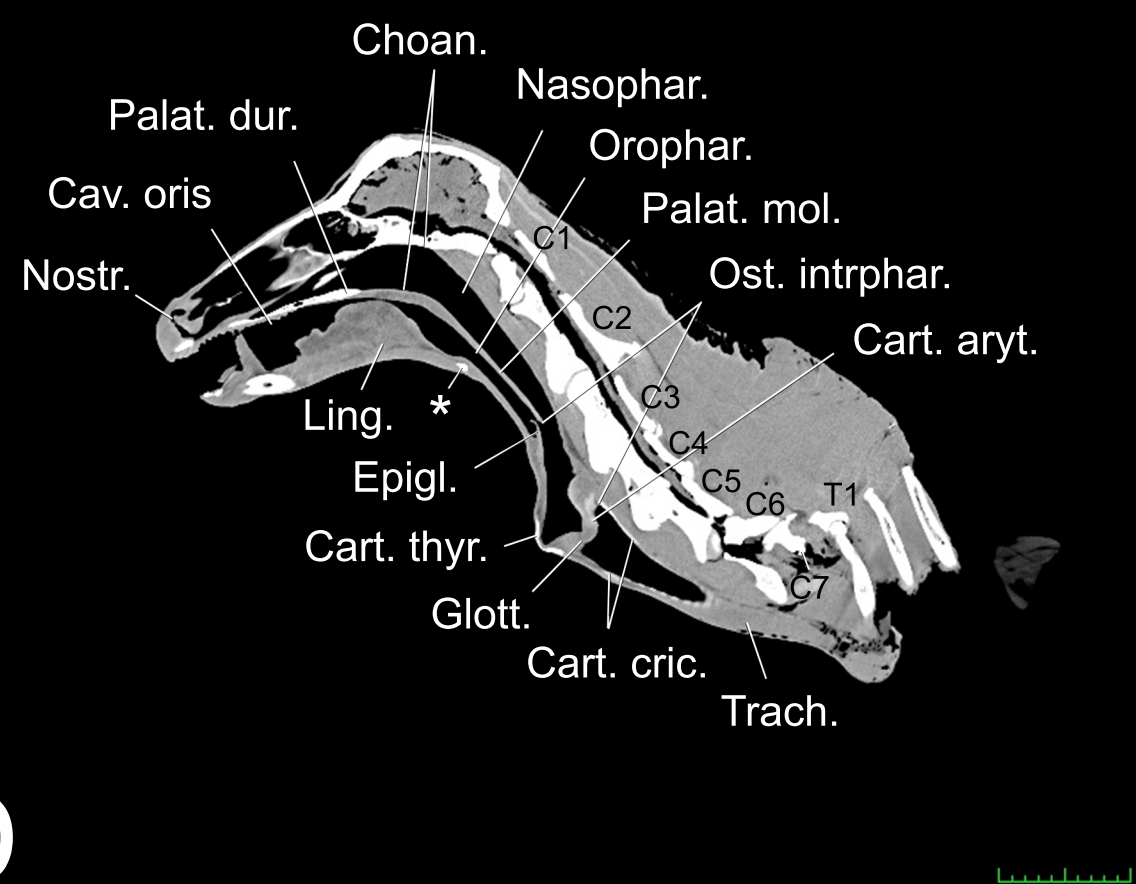
842

A

hyoid
apparatus

larynx

B

hyoid
apparatus

larynx

(A) Male 1

Common laryngopharyngeal tract
Nasopharynx and nasal cavity
Oropharynx and oral cavity

(B) Male 2

Common laryngopharyngeal tract
Nasopharynx and nasal cavity
Oropharynx and oral cavity