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Radiographic analysis of vocal tract length and its relation to overall body size in two canid species

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Abstract

Body size is an important determinant of resource and mate competition in many species. Competition is often mediated by conspicuous vocal displays, which may help to intimidate rivals and attract mates by providing honest cues to signaler size. Fitch proposed that vocal tract resonances (or formants) should provide particularly good, or honest, acoustic cues to signaler size because they are determined by the length of the vocal tract, which in turn, is hypothesized to scale reliably with overall body size. There is some empirical support for this hypothesis, but to date, many of the effects have been either mixed for males compared with females, weaker than expected in one or the other sex, or complicated by sampling issues. In this paper, we undertake a direct test of Fitch's hypothesis in two canid species using large samples that control for age- and sex-related variation. The samples involved radiographic images of 120 Portuguese water dogs *Canis lupus familiaris* and 121 Russian silver foxes *Vulpes vulpes*. Direct measurements were made of vocal tract length from X-ray images and compared against independent measures of body size. In adults of both species, and within both sexes, overall vocal tract length was strongly and significantly correlated with body size. Effects were strongest for the oral component of the vocal tract. By contrast, the length of the pharyngeal component was not as consistently related to body size. These outcomes are some of the clearest evidence to date in support of Fitch's hypothesis. At the same time, they highlight the potential for elements of both honest and deceptive body signaling to occur simultaneously via differential acoustic cues provided by the oral versus pharyngeal components of the vocal tract.

Keywords

body size; vocal tract length; animal communication

Introduction

Body size is a general feature of organismal biology with broad behavioral significance. In many species, successful competition for food or mating opportunities is determined in part by differences in body size (reviewed in Fairbairn, Blanckenhorn & Székely, 2007). Such body size-related competition is often mediated indirectly through the use of distinctive vocalizations. For example, males of many species produce loud vocalizations when competing aggressively with rival males or when courting females (e.g. Fitch & Reby, 2001;

Pfefferle & Fischer, 2006; Sanvito, Galimberti & Miller, 2007). These vocal signals can by themselves play a role in intimidating rivals and attracting females by indirectly signaling body size (Fitch, 1997; Reby & McComb, 2003; Reby *et al.*, 2005; Charlton, Reby & McComb, 2007; Taylor, Reby & McComb, 2010; Charlton *et al.*, 2011). Thus, a central theme in animal communication concerns the extent to which core elements of vocal anatomy scale reliably with body size and thus generate honest acoustic cues to signaler size, a subject termed ‘acoustic allometry’ (cf. Fitch, 2000a; Rendall *et al.*, 2005).

Here, a core focus of research specifically targets the resonances of the vocal tract. This focus follows from the source-filter theory of human voice production (Fant, 1960), where voice resonances, or formants, are a straightforward consequence of the length and cross-sectional area of the vocal tract (reviewed for animals by Taylor & Reby, 2010). Building on this logic, Fitch (1997, 2000b) proposed that formants could be a reliable source of cues to body size because they are determined by the length of the vocal tract, which in turn, is predicted to scale reliably with overall body size.

There have been a number of tests of Fitch’s hypothesis involving a variety of species (reviewed in Table 1). Most studies have involved evaluating the relationship between body size and formants measured from recorded vocalizations. These studies are consistent in finding clear size-related differences in formants between adult males and females, and between adults of either sex and juvenile or immature individuals (e.g. Fitch, 1997; Pfefferle & Fischer, 2006). As a result, it is now fairly clear that the general developmental trajectory for most species involves correlated growth in overall body size and vocal tract length from infancy to adulthood. Some studies have also confirmed additional size-related formant differences within age–sex classes (e.g. Fitch & Reby, 2001; Reby & McComb, 2003; Rendall *et al.*, 2005; Charlton *et al.*, 2011), such as within adult males or within adult females. However, the magnitude of the effects at this level generally have been much smaller or, in some cases, entirely absent (e.g. van Dommelen & Moxness, 1995; Griesbach, 1999; Gonzalez, 2004; Bruckert *et al.*, 2005; Rendall *et al.*, 2005; Charlton, Zhang & Snyder, 2009). As a result, the acoustic allometric relationships within age–sex classes may be weaker or more equivocal.

Very few studies have tested the hypothesis by more direct examination of the relationship between body size and the length of the vocal tract. Fitch & Giedd (1999) conducted a unique magnetic resonance imaging study of humans to get direct measures of vocal tract length for comparison with measures of body size, and Riede & Fitch (1999) conducted a similar analysis for domestic dogs using X-ray images. Both studies reported strong correlations between vocal tract length and body size. In humans, the relationship was especially strong across age–sex classes, with adults being substantially taller and heavier than either infants, juveniles or adolescents and also having substantially longer vocal tracts. In dogs, the relationship was tested across age–sex classes and also across different breeds ranging from some of the smallest breeds available (e.g. dachshund, pekingese and shi tzu) to some of the largest (e.g. German shepherd, doberman, rottweiler). Across the large range of body sizes thus represented, there were very strong correlations between body size and X-ray measures of vocal tract length. Once again, the strength of the allometric relationships within age–sex classes, or within particular breeds, is less clear.

Taken together, the logic of Fitch’s hypothesis of voice-based body size cueing is compelling and there is some supporting evidence. To date, much of that evidence concerns the relationship between body size and formants measured from recorded vocalizations with only two studies examining the relationship via direct measures of vocal tract length. Further, in both kinds of studies, research has consistently confirmed strong allometric relationships across age–sex classes, but the strength of the relationships within particular

age–sex classes is more equivocal. In this paper, we attempt to help fill both gaps using unique radiographic samples of a large number of adult males and females belonging to two different canid species. The goal is to make direct measures of vocal tract length for comparison with overall body size and to do so within both adult males and adult females, thereby controlling important age- and sex-related variation in both anatomical features to allow a direct and cleaner test of Fitch's hypothesis.

Materials and methods

Subjects

Two independent samples were used. The first sample involved radiographic images of the upper body and head of a large sample of Portuguese water dogs *Canis lupus familiaris* (hereafter PWD). This breed was originally bred and utilized by fisherman in the Portuguese fishing fleet (Chase *et al.*, 1999). The breed experienced a catastrophic decline in the first half of the 20th century, and the current world stock is traceable to a small founder population of 31 individuals following World War II. The breed is the subject of a unique research program (the Georgie Project), in which the pedigree of all descendants from the founder population is known across 26 generations. Detailed morphological, physiological, sereological, histological, genotypic and life-history data have been collected for a large number of individuals in the database allowing detailed genomic studies of many traits (Chase *et al.*, 2002, 2011).

Radiograph images were made on anesthetized dogs attending veterinary clinics for surgical procedures. None were known to have suffered injuries that would affect vocal anatomy. Imaging was done in the parasagittal plane in a standardized position, with a coin placed on the imaging table to allow size standardization. The radiographic sample involved 547 individuals, but many were omitted because images were of insufficient clarity to allow accurate identification of vocal tract landmarks. Many others were omitted because the dogs were still intubated from surgery when radiographs were made, which might distort natural vocal tract proportions. From the remaining sample of non-intubated dogs, we selected a balanced set of 60 individuals of each sex. All individuals were adults (older than 2 years), 62 of which (51%) had been spayed or neutered. Possible effects of the latter on body growth were examined using a multivariate analysis of variance test of spay/neuter status on femur and humerus length and body mass. There were no effects for either sex (females: $F_{1,56} = 0.68$, $P = 0.569$; males: $F_{1,57} = 0.404$, $P = 0.751$).

The second sample involved whole body radiographs of 121 Russian silver foxes, a melanistic variant of the red fox *Vulpes vulpes*. Silver foxes have been systematically managed and bred for many years in Russia, largely for the commercial fur trade. However, since 1959, the foxes have also been selectively bred specifically for temperament to investigate the process of domestication (e.g. Trut *et al.*, 2006; Kukekova *et al.*, 2011). Imaging was done in the parasagittal plane and standardized for all individuals. The sample involved a nearly balanced set of 64 females and 57 males, none of which were known to have been spayed or neutered.

Anatomical measures

Multiple measures of body size were made previously and reported in Chase *et al.* (2002). For this study, we used the length of two long bones (femur and humerus) and body mass as metrics of size. To obtain measures of vocal tract length, we subdivided the vocal tract into two components, an anterior (rostral) component corresponding roughly to the oral portion of the vocal tract and a posterior (caudal) component corresponding to the non-oral (or pharyngeal) portion of the vocal tract. The rostral boundary of the oral component was

defined as the tips of the upper incisors, which were clearly visible on all images. The caudal boundary of the oral cavity is delineated by the hard and soft palates, but these were sometimes difficult to identify clearly. The bulla tympanica, which as a bony structure, was clearly visible in all images and is situated immediately adjacent to the temporo-mandibular joint, was therefore used as a reliable and easily identifiable index of the junction between the oral and pharyngeal components of the vocal tract. The caudal boundary of the pharyngeal component of the vocal tract was defined in two ways using either the basihyoid bone or the dorsal aspect of the cricoid cartilage to capture, respectively, its ventral and dorsal aspects. Measures of overall vocal tract length based on the hyoid as the caudal boundary were subsequently labeled as VTL_H and measures of overall vocal tract length based on the cricoid as the caudal boundary were subsequently labeled VTL_C .

Sample radiographs of a PWD and a fox are shown in Figs 1 and 2 with labels illustrating the vocal tract landmarks and the distances between them. PWD and fox images were measured identically with one exception: for the PWD sample, measures of the dorsal aspect of the pharyngeal component were taken from the midpoint of the dorsal margin of the cricoid cartilage, whereas for the fox sample, the most caudal margin of the cricoid cartilage was used.

All measurements were made using NIH Image (version 1.44o, Research Services Branch of the National Institutes of Health (NIH), Bethesda, MD, USA) and recorded in number of pixels. To evaluate measurement reliability, 10 images were randomly selected for re-measurement of each vocal tract dimension with a different set of 10 images selected for each dimension. This procedure involved re-measuring approximately 10% of the sample. The difference between original and re-measured values was generally very low, with the mean absolute value of the differences being only 3.42 pixels [standard deviation (sd) = 4.75] or 1.76%.

Head position

Procedures for making radiographic images were standardized such that the animals' position and posture on the X-ray table were similar for all individuals, with two exceptions. One exception concerned the degree of extension or flexion of the head (Fig. 3). The degree to which head extension affects laryngeal position in sedated dogs or foxes is unknown, but it is known to affect laryngeal position in awake humans and in sedated horses (Hellsing, 1989; McCluskie *et al.*, 2008). To evaluate and control for possible effects due to variable head extension, we measured the angle between a line connecting bulla to incisors and a second line through the vertebral canal for each individual (see Fig. 1). This angle characterizes the degree to which the head was extended or flexed in each image.

A second exception concerned rotation (eversion) of the head along its long (rostral-caudal) axis. In some cases, an individual's head was rotated downward into the table because the caudal aspect of the head (at the ears) is wider than the rostral aspect (at the nose) such that, in an anesthetized animal, the nose can turn downward toward the table. This effect was made obvious in X-ray images by the visibility of both the left and right bulla in some images. To control for possible influences on vocal tract length calculations when an animal's head was rotated, we measured each vocal tract dimension to both the left and the right bulla and averaged the two measures.

Results

General body size and vocal tract characteristics

Descriptive statistics for all anatomical measures are provided in Tables 2 and 3. There was significant sexual dimorphism in both body size and vocal tract dimensions in both species, with males being larger than females. Dimorphism values were generally consistent and similar for all traits and both species at 5–7% for linear dimensions (except hyoid–bullae and cricoid–bullae in foxes where dimorphism values were nearly doubled to 11%) and 15–20% for body mass (a volumetric dimension).

Trait correlations were consistent and similar in the two species and for both sexes (Tables 4 and 5). All three body size measures were significantly and strongly correlated. Predictably, the correlations were somewhat higher between the two measures of long bone length ($r = 0.72$ – 0.90) than between either of these and body mass ($r = 0.34$ – 0.64). The two measures of overall vocal tract length were also highly correlated (VTL_H and VTL_C ; $r = 0.84$ – 0.96) and both were also significantly correlated with all measures of body size, although the magnitude of the correlations was more variable and often smaller ($r = 0.42$ – 0.71). The constituent components of the vocal tract were also significantly correlated with one another, but the magnitude of the correlations was larger between the two pharyngeal component measures (hyoid–bullae and cricoid–bullae; $r = 0.52$ – 0.79) than between either of these measures and the single oral component measure (Bullae–Incisor; $r = 0.26$ – 0.37). Measures of the constituent components of the vocal tract correlated variably and sometimes non-significantly with measures of body size. For example, bullae–incisor was significantly and often strongly correlated with all measures of body size ($r = 0.29$ – 0.75), while the correlations for hyoid–bullae and cricoid–bullae were generally weaker ($r = 0.26$ – 0.58) and often not significant for one or the other sex and sometimes both.

Effects of head position on vocal tract dimensions

The degree of head extension (or flexion) varied among images. The variation was greater for the PWD sample, where the angle between head and spinal axes ranged from 85–164 degrees (males: $M = 118.9$, $SD = 13.8$; females: $M = 121.7$, $SD = 14.2$), while for the fox sample this angle ranged from 56–94 degrees (males: $M = 71.1$, $SD = 7.5$; females: $M = 77.8$, $SD = 7.0$). In separate bivariate regressions, this angle significantly affected measures of hyoid–bullae and cricoid–bullae for males and hyoid–bullae for females in the PWD sample, and significantly affected measures of bullae–incisor in the female fox sample (see Tables 2 and 3 for statistics), although in no case did head position explain more than 12% of the variance in these vocal tract dimensions. Effects were nearly significant for measures of cricoid–bullae and VTL_H for females in the fox sample, but not significant for the remaining vocal tract dimensions.

To generate unbiased measures of all vocal tract dimensions for further analyses of their relationships with overall body size, we used the residuals from these bivariate regressions.

Effects of body size on vocal tract dimensions

After removing the effects of head position on vocal tract dimensions, the influence of body size on these dimensions was tested in separate multiple regressions, in each case using humerus and femur length and body mass as independent variables. Results are shown in Figs 4 and 5 as well as Tables 6 and 7. For males and females of both species, body size had a significant influence on both measures of overall vocal tract length (VTL_H and VTL_C), explaining between 29 and 58% of their variance.

Effects of body size on constituent components of vocal tract length were more variable. For the PWD sample, body size had a significant effect on the length of the oral component of the vocal tract (bullae–incisor), explaining 46 and 55% of its variance in males and females, respectively. However, body size had less consistent effects on the length of either measure of the pharyngeal component of the vocal tract (hyoid–bullae or cricoid–bullae), being significant for only one measure in males (hyoid–bullae; see Table 6 for detailed statistics). In the fox sample, body size significantly influenced the oral component of the vocal tract (bullae–incisor), explaining 37 and 31% of its variance in males and females. Body size also significantly influenced the length of both pharyngeal components of the vocal tract (hyoid–bullae and cricoid–bullae) in males but only one of these (cricoid–bullae) in females, and generally accounted for less variance (13 and 37%).

Discussion

Our results show a consistent and positive relationship between body size and the length of the vocal tract in both the adult males and the adult females of two canid species. This is an important finding. As reviewed in the Introduction, previous research has helped to establish that variation in vocal tract length tracks the relatively large body size differences that exist between age–sex classes in many species. However, it has not established so clearly that vocal tract length also tracks the much smaller degree of variation in body size that occurs among individuals within age–sex classes. Our results are thus important in showing that vocal tract length can indeed track subtler body size variation at this level, thereby providing additional support for Fitch's (1997) hypothesis of honest body size signaling.

The size-related effects we observed were stronger for some components of the vocal tract compared with others, however. In both the dog and fox samples, the oral component of the vocal tract was strongly influenced by body size, but the effects were weaker and less consistent for the pharyngeal component. This pattern suggests there might be some independence in growth of these two components (Lieberman *et al.*, 2001; Nishimura *et al.*, 2003; Vorperian *et al.*, 2009, 2011). Such independence might reflect differential physiological or developmental constraints. The oral component is completely surrounded by the bony anatomy of the face and skull. Hence, its size will track variation in overall body size to the extent that cranio-facial growth programs do. In contrast, the length of the pharyngeal component is determined primarily by the position of the larynx, which may be freer to vary independently of body size because it is not so rigidly defined by, or attached to, surrounding bony anatomy. Instead, the position of the larynx is influenced by the anatomy of pharyngeal and extrinsic laryngeal musculature and the hyoid skeleton, which together allow some laryngeal freedom. For example, in red deer, the ligamentous connection between the larynx and the hyoid skeleton allows for dramatic descent of the larynx during vocalization, while evidence from several other species confirms more modest dynamic, or permanent, descent of the larynx in the vocal tract (Fitch & Giedd, 1999; Fitch & Reby, 2001; Weissengruber *et al.*, 2002; Nishimura *et al.*, 2003; Sanvito *et al.*, 2007; Frey & Riede, 2013).

This difference in potential growth constraints on oral versus pharyngeal components of the vocal tract might help to account for some of the equivocal effects reported previously (Howard & Young, 1998; Griesbach, 1999; Gonzalez, 2004; Bruckert *et al.*, 2005; Rendall *et al.*, 2005) if, in estimating overall vocal tract length, the uncorrelated effects of one component of the vocal tract have sometimes obscured correlated effects because of the other. There are other anatomical factors that might also complicate matters, including variability in the cross-sectional area of vocal tract cavities and in the potential coupling of sub-glottal cavities, air sacs, or side-branches, such as nasal cavities (Story, Titze & Hoffman, 1996; Riede & Fitch, 1999; Riede *et al.*, 2008).

Collectively, these issues bear on an additional element of Fitch's hypothesis of voice-based body size signaling, namely that it is open to deception. As Fitch himself emphasizes, the relative emancipation of laryngeal position opens the door to deceptive body size signaling (Fitch, 1999, 2000b, 2010). Organisms that can lower their larynx, either dynamically during vocalization, as in red deers and some other species, or permanently, as in humans, can thereby create a longer vocal tract than they would otherwise be expected to have (Fitch, 1999, 2000b; Fitch & Giedd, 1999; Fitch & Reby, 2001). They can thus project in the reduced formants of their vocalizations an exaggerated impression of their body size. Such potential for size deception has been assumed to be grounded in the effects of variable laryngeal descent on the length of the entire vocal tract. However, our results suggest that it could be linked primarily to the pharyngeal component of the vocal tract as the component most directly influenced by laryngeal position, or possibly also arise from additional non-uniformities in vocal tract geometry like those noted earlier.

This inference has two important implications for theory and research. First, it might not always be possible to establish for a given species that vocal signals are categorically either 'honest' or 'dishonest' with respect to body size cueing. Instead, it is possible they might often be both if acoustic cues arising from the action of one component provide relatively accurate cues to signaler size while cues from the other component do not. This may create an additional important selective pressure on receivers to be able to discriminate between the honest and dishonest components of a particular signal. An important corollary is that separating the contributions to the acoustic structure of signals of the oral versus pharyngeal components of the vocal tract, and also considering the additional roles of cross-sectional area and possibly side branches, might allow future work to identify and distinguish the co-occurrence of honest and dishonest elements of body size signaling in particular species.

Two final caveats should be noted. First, our findings pertain only to the physical relationships between vocal tract dimensions and body size. They do not address the extent to which the vocalizations produced by either species necessarily preserve the physical relationships observed. In particular, laryngeal position might be different in active, behaving animals compared with the anaesthetized animals studied, and further, it might be modified dynamically during vocal production (Fitch, 2000c). Dynamic movement of the larynx while vocalizing would alter the length of the pharyngeal component of the vocal tract, which might further weaken its correlation with body size. Alternatively, such laryngeal movement might actually introduce a stronger relationship with body size and, in this way, increase or restore 'honesty' in the cueing of body size vis a vis the pharyngeal component of the vocal tract as well.

An additional caveat concerns the finding that head position can affect measures of vocal tract length. This was particularly pronounced in measures of pharyngeal cavity length, likely because variable head extension (or flexion) involves stretching (or relaxing) muscular attachments to the laryngeal complex, thereby elevating (or lowering) the body of the larynx. This is an important factor for researchers to be cognizant of, and attempt to control, in future imaging studies examining vocal tract dimensions. It is also important vis-a-vis the natural vocal behavior of the species, where variable head extension or flexion may be involved in the production of different vocalizations. Altering laryngeal position (or other features of laryngeal action) and thus vocal tract dimensions may influence the extent to which the resulting voice cues reliably reflect the caller's size.

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Figure 1.

Radiograph of head and vocal tract of Portuguese water dog illustrating vocal tract landmarks and distances between them used to evaluate overall vocal tract length and the length of constituent components of the vocal tract. (1) basihyoid; (2) cricoid; (3) bulla tympanica; (4) incisors; (A) hyoid–bulla distance; (B) cricoid–bulla distance; (C) bulla–incisor distance; (D) spinal axis.

Figure 2. Radiographs of the upper body (top) and zoomed head and vocal tract regions (bottom) of foxes illustrating vocal tract landmarks and distances between them used to evaluate overall vocal tract length and the length of constituent components of the vocal tract. Landmarks and distances are the same as those labelled in Fig. 1.

Figure 3. Radiographs of Portuguese water dogs illustrating variation in the degree of head extension or flexion quantified as the angle of deviation from the spinal axis. (a) 164°; (b) 128°; (c) 87°.

Figure 4. Relationship between body size (humerus length) and vocal tract length measurements in Portuguese water dog sample. Vocal tract length measurements have been corrected for the effects of head position.

Figure 5. Relationship between body size (humerus length) and vocal tract length measurements in fox sample. Vocal tract length measurements have been corrected for the effects of head position.

Table 1

Summary of past studies of relationships between body size, vocal tract length, and voice formants

Author(s)	Species	Major findings
Bruckert <i>et al.</i> (2005)	Humans	No correlation between formants and body size.
Charlton <i>et al.</i> (2009)	Giant pandas	Correlation between formants and body weight in males but not females.
Charlton <i>et al.</i> (2011)	Koalas	Correlation between formants and body size in males.
Fitch (1997)	Rhesus macaques	Correlation between body size, vocal tract length, and formant dispersion.
Fitch & Giedd (1999)	Humans	Correlations between height, weight and vocal tract length.
Fitch (2000c)	Primates and carnivores	Correlation between weight and palate length.
Fitch & Reby (2001)	Red deer	Correlation between vocal tract length and formants.
Gonzalez (2004)	Humans	Weak relationship between body size and formants.
Griesbach (1999)	Humans	Weak relationship between height and formants.
Howard & Young (1998)	American toad	Correlation between body size and dominant frequency in males.
Perry, Ohde & Ashmead (2001)	Humans	Correlation between body size and formants.
Peters <i>et al.</i> (2009)	Various feline species	Correlation between body weight and mean dominant frequency.
Pfefferle & Fischer (2006)	Hamadryas baboon	Correlation between body size and formant dispersion.
Pfefferle <i>et al.</i> (2007)	Lions	Correlation between chest circumference and formants.
Reby & McComb (2003)	Red deer	Correlation between body weight and lowest formants.
Rendall <i>et al.</i> (2005)	Humans and baboons	Correlation between height and formants in males but not females.
Riede & Fitch (1999)	Domestic dogs	Correlation between body mass, skull length and vocal tract length and formant dispersion.
Sanvito <i>et al.</i> (2007)	Elephant seals	Correlation between body length and formants.
van Dommelen & Moxness (1995)	Humans	No correlation between body size and formants.
Wilczynski, Keddy-Hector & Ryan (1992)	Cricket frogs	Correlation between body size and dominant frequency.

Table 2

Descriptive statistics and head position effects for Portuguese water dog sample

Measurement	Mean ^a (range)		M : F dimorphism	T-test ^b t-value (P-value)	Head position F-value and R ² (P-value)	
	Male	Female			Male	Female
Mass	24.3 (16–35)	21.0 (15–31)	1.16	$t = -4.771$ ($P < 0.001$)	N/A	N/A
Humerus	414.7 (348–469)	390.6 (314–442)	1.06	$t = -5.15$ ($P < 0.001$)	N/A	N/A
Femur	491.9 (420–556)	477.0 (387–537)	1.03	$t = -4.39$ ($P < 0.001$)	N/A	N/A
Bulla–incisor	468.4 (402–531)	442.2 (382–512)	1.06	$t = -4.98$ ($P < 0.001$)	$F = 0.03$; $R^2 = 0.001$ ($P = 0.862$)	$F = 1.27$; $R^2 = 0.021$ ($P = 0.265$)
Hyoid–bullae	156.1 (123–185)	145.5 (100–184)	1.07	$t = -3.69$ ($P < 0.001$)	$F = 7.64$; $R^2 = 0.115$ ($P = 0.008$)	$F = 4.24$; $R^2 = 0.068$ ($P = 0.044$)
Cricoid–bullae	163.0 (111–197)	152.4 (98–205)	1.07	$t = -3.26$ ($P < 0.001$)	$F = 5.54$; $R^2 = 0.087$ ($P = 0.022$)	$F = 0.76$; $R^2 = 0.013$ ($P = 0.388$)
VTL _H	624.5 (528–706)	587.8 (507–689)	1.06	$t = -5.36$ ($P < 0.001$)	$F = 1.35$; $R^2 = 0.022$ ($P = 0.249$)	$F = 3.09$; $R^2 = 0.051$ ($P = 0.084$)
VTL _C	631.0 (517–710)	594.3 (518–694)	1.06	$t = -5.37$ ($P < 0.001$)	$F = 1.44$; $R^2 = 0.024$ ($P = 0.235$)	$F = 1.30$; $R^2 = 0.022$ ($P = 0.259$)

^a Mean and range values for body mass are given in kilograms and in number of pixels for all other measures.^b T-test for sex difference.

Table 3

Descriptive statistics and head position effects for fox sample

Measurement	Mean ^a (range)		M : F dimorphism	T-test ^b <i>t</i> -value (<i>P</i> -value)	Head position <i>F</i> -value and <i>R</i> ² (<i>P</i> -value)	
	Male	Female			Male	Female
Mass	5.1 (4.2–6.0)	4.3 (3.8–5.4)	1.19	$t = -15.04$ ($P < 0.001$)	N/A	N/A
Humerus	341.2 (315–360)	318.7 (298–335)	1.07	$t = -13.85$ ($P < 0.001$)	N/A	N/A
Femur	320.2 (300–337)	303.3 (278–321)	1.06	$t = -12.38$ ($P < 0.001$)	N/A	N/A
Bulla-Incisor	319.0 (302–340)	304.5 (291–319)	1.05	$t = -12.99$ ($P < 0.001$)	$F = 0.19$; $R^2 = 0.003$ ($P = 0.663$)	$F = 6.01$; $R^2 = 0.088$ ($P = 0.017$)
Hyoid-Bulla	80.7 (73–90)	72.7 (65–79)	1.11	$t = -12.08$ ($P < 0.001$)	$F = 0.41$; $R^2 = 0.007$ ($P = 0.527$)	$F = 0.03$; $R^2 = 0.000$ ($P = 0.874$)
Cricoid-Bulla	96.5 (83–113)	87.1 (75–101)	1.11	$t = -9.20$ ($P < 0.001$)	$F = 0.45$; $R^2 = 0.008$ ($P = 0.506$)	$F = 3.45$; $R^2 = 0.053$ ($P = 0.068$)
VTL _H	399.7 (381–429)	377.3 (361–396)	1.06	$t = -15.57$ ($P < 0.001$)	$F = 0.37$; $R^2 = 0.007$ ($P = 0.546$)	$F = 3.75$; $R^2 = 0.057$ ($P = 0.058$)
VTL _C	415.5 (387–441)	391.6 (377–414)	1.06	$t = -15.52$ ($P < 0.001$)	$F = 0.49$; $R^2 = 0.009$ ($P = 0.488$)	$F = 0.35$; $R^2 = 0.006$ ($P = 0.559$)

^a Mean and range values for body mass are given in kilograms and in number of pixels for all other measures.^b *T*-test for sex difference.

Table 4

Pearson correlations for body size and vocal-tract length variables for Portuguese Water Dog sample

	Sex	Bulla-incisor	Hyoid-bulla	Cricoid-bulla	VTL _H	VTL _C	Femur	Humerus
Bulla-Incisor	F							
	M							
Hyoid-Bulla	F	0.369 [*]						
	M	0.369 [*]						
Cricoid-Bulla	F	0.256 [*]	0.767 ^{**}					
	M	0.194	0.788 ^{**}					
VTL _H	F	0.911 ^{**}	0.719 ^{**}	0.532 ^{**}				
	M	0.932 ^{**}	0.680 ^{**}	0.460 ^{**}				
VTL _C	F	0.890 ^{**}	0.642 ^{**}	0.668 ^{**}	0.952 ^{**}			
	M	0.880 ^{**}	0.676 ^{**}	0.637 ^{**}	0.955 ^{**}			
Femur	F	0.751 ^{**}	0.252	0.146	0.673 ^{**}	0.653 ^{**}		
	M	0.413 ^{**}	0.239	0.332 [*]	0.419 ^{**}	0.484 ^{**}		
Humerus	F	0.710 ^{**}	0.217	0.180	0.627 ^{**}	0.634 ^{**}	0.898 ^{**}	
	M	0.572 ^{**}	0.284 [*]	0.306 [*]	0.561 ^{**}	0.593 ^{**}	0.722 ^{**}	
Mass	F	0.525 ^{**}	0.157	-0.007	0.462 ^{**}	0.407 ^{**}	0.636 ^{**}	0.609 ^{**}
	M	0.635 ^{**}	0.428 ^{**}	0.321 [*]	0.668 ^{**}	0.652 ^{**}	0.450 ^{**}	0.592 ^{**}

* $P < 0.05$;** $P < 0.001$.

Table 5

Pearson correlations for body size and vocal-tract length variables for fox sample

	Sex	Bulla-incisor	Hyoid-bulla	Cricoid-bulla	VTL _H	VTL _C	Femur	Humerus
Bulla-Incisor	F							
	M							
Hyoid-Bulla	F	0.116						
	M	0.347*						
Cricoid-Bulla	F	-0.066	0.591**					
	M	0.234	0.586**					
VTL _H	F	0.888**	0.559**	0.218				
	M	0.918**	0.692**	0.428**				
VTL _C	F	0.732**	0.494**	0.631**	0.839**			
	M	0.809**	0.586**	0.761**	0.872**			
Femur	F	0.588**	0.063	0.275*	0.519**	0.645**		
	M	0.582**	0.385*	0.530**	0.612**	0.710**		
Humerus	F	0.569**	0.209	0.243	0.572**	0.608**	0.797**	
	M	0.479**	0.440**	0.579**	0.556**	0.670**	0.766**	
Mass	F	0.292*	0.255*	0.262*	0.361*	0.406**	0.542**	0.541**
	M	0.378*	0.474**	0.382*	0.492**	0.484**	0.339*	0.463**

* $P < 0.05$;** $P < 0.001$.

Table 6

Results of multiple regression tests for effects of body size on overall vocal tract length and on constituent components of vocal tract length for Portuguese water dog sample

Vocal tract measure	Sex	<u>Effects of size</u>		
		<i>F</i> -value	<i>R</i> ²	<i>P</i>
VTL _H	M	16.693	0.468	<0.001
	F	13.910	0.427	<0.001
VTL _C	M	16.740	0.473	<0.001
	F	13.897	0.431	<0.001
Bulla-Incisor	M	16.071	0.458	<0.001
	F	22.569	0.547	<0.001
Hyoid-Bulla	M	3.863	0.169	0.014
	F	0.893	0.046	0.451
Cricoid-Bulla	M	2.462	0.117	0.072
	F	1.026	0.053	0.388

Table 7

Results of multiple regression tests of effects of body size on overall vocal tract length and on constituent components of vocal tract length for fox sample

Vocal tract measure	Sex	<u>Effects of size</u>		
		<i>F</i> -value	<i>R</i> ²	<i>P</i>
VTL _H	M	15.301	0.464	<0.001
	F	8.227	0.291	<0.001
VTL _C	M	23.905	0.575	<0.001
	F	14.345	0.418	<0.001
Bulla–incisor	M	10.549	0.374	<0.001
	F	9.158	0.314	<0.001
Hyoid–bullae	M	7.203	0.290	<0.001
	F	2.707	0.119	0.053
Cricoid–bullae	M	9.862	0.358	<0.001
	F	3.232	0.139	0.028