RADIOGRAPHIC ANALYSIS OF CANINE VOCAL TRACT ANATOMY AND ITS IMPLICATIONS FOR HUMAN LANGUAGE ORIGINS

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Abstract

Radiographic images of the skull and vocal tract of adults from two canid species were analyzed for two studies addressing functional issues in animal communication and human language. Study 1 tested the hypothesis that vocal tract length scales reliably with overall body size such that the acoustic features of vocalizations influenced by vocal tract length can serve as honest cues to vocalizer body size. Results supported this hypothesis but emphasized that correlations with body size were better for oral cavity length than for pharyngeal cavity length. Study 2 tested the hypothesis that laryngeal position can vary in response to selection on cranio-facial size and shape. Results supported this hypothesis, finding that the larynx occupies a more descended position in the vocal tract of individuals with shorter, broader faces compared to longer, narrower faces. The latter findings have important implications for the origins and evolution of language in humans.

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Chapter 1

Structure-Function Relationships in Body Size Signaling in Animals

1.1 Competition and Body Size

Competition for resources and mating opportunities is ubiquitous, and success in such competition is often mediated by body size where larger individuals are often more successful in competition than smaller individuals (Peters, 1983; Schmidt-Nielson, 1984; Harvey, 1990; Alexander, 1996; Fitch, 1997).

An especially common and important context for competition influenced by body size is that which occurs over access to mates. Mate competition is a two-sided coin: members of one sex (often males) compete to exclude one another from mating (intrasexual competition), and members of this sex also compete for the attention of the opposite sex (often females) who sometimes exercise some choice in mating (intersexual competition: Darwin, 1859, 1871).

In both contexts, larger body size may be advantageous because larger males are better able to exclude smaller rivals from the mating arena (Clutton-Brock, Harvey, & Rudder, 1977); also, females may prefer large-bodied males because large body size effectively signals a male's ability to monopolize a larger share of limited resources in order to sustain the costs of growing large. Indeed, there is evidence from a wide variety of species in support of both points (Clutton-Brock, Harvey, & Rudder, 1977; Simmons, 1988; Fischer & Lara, 1999).

1.1.1 Signaling Large Body Size

The universality of competition favoring larger body size has led to Cope's Law which states that, over evolutionary time, species tend towards larger and larger size in a race to *out-size* the competition (LaBarbera, 1989). This pattern of size evolution frequently also leads to body size dimorphism with males often larger than females in many species, particularly mammals (Fairbairn, 1997).

It is also the case that competitors generally prefer to avoid physical confrontation because it is energetically expensive and risks injury. Hence, selection on body size sets up associated selection to advertise size indirectly. Examples from non-human primates include male baboons producing loud 'wahoo' calls during dominance displays and when competing for access to females (Fischer, Hammerschmidt, Cheney, & Seyfarth, 2002) as well as Rhesus Macaques producing aggressive 'pant-threats' that are related to body size (Fitch, 1997). Among amphibians, many toads produce loud mating calls to attract females. Davies and Halliday (1978) found that larger bodied males produce lower fundamental frequency mating calls and Howard and Young (1998) found that females attend to and prefer callers with a lower dominant frequency.

1.2 The Anatomy of Vocal Production

The capacity for indirect vocal advertisement of body size is intimately tied to the vocal anatomy of the species, which in most organisms can be modeled as having two primary components, a source of sound production and a subsequent filter of that sound (Fant, 1960).

1.2.1 The Acoustic Source

For many animals, the source of sound involves the larynx. Tissues in the larynx (the vocal folds) vibrate as the air exhaled from the lungs passes across them. The resulting voiced sound often (but not always) involves regular oscillations of the vocal fold tissues creating a harmonic sound whose base frequency is termed the *fundamental frequency* (and is often abbreviated as F_0). The F_0 of voiced sounds is the basis for our percept of voice *pitch.*

A primary factor determining the rate of vocal fold vibration is the length of the vocal folds (Titze, 1989). Longer vocal folds naturally oscillate at lower rates, while shorter vocal folds naturally oscillate at higher rates. Common examples of the differences in baseline vocal fold oscillation are evidenced in the lower voice pitch of adult men compared to women and women compared to children which are ultimately traceable to the differences in vocal fold length between them (Titze, 1989).

1.2.2 The Acoustic Filter

The second key component of the vocal production system concerns the vocal tract cavities above the larynx, which act as acoustic filters of the sounds emanating from the laryngeal source (Fant, 1960). As the laryngeally produced sound travels up the vocal tract, energy at some frequencies readily propagates because it coincides with the natural resonances of the vocal tract cavities, while energy at other frequencies is absorbed by the walls of the vocal tract. Those frequencies that pass readily – that coincide with the vocal tract resonances – are referred to as the resonant frequencies of the sounds (sometimes referred to as ‘formants’ and denoted F_n). An important determinant of the resonant frequencies of laryngeally produced sounds is the overall size of the vocal tract through which the sounds propagate, and particularly the vocal tract’s length. Larger, longer vocal tracts have lower natural resonance frequencies, while smaller, shorter vocal tracts have higher natural resonance frequencies.

A good metaphor for appreciating these filter effects of the vocal tract concerns musical instruments and, in particular, the difference in timbre between large horns, like the tuba, and small horns, like the trumpet. The tuba produces very low-frequency sounds because it's large horn holds a relatively large mass of air, which naturally resonates at relatively low frequencies. In contrast, the smaller horn of the trumpet holds a relatively small mass of air, which naturally resonates at higher frequencies. These frequency differences are illustrated dynamically in the action of a single, horned instrument, the trombone. As a trombone is played, the player will move the "slide" back and forth to modify the timbre (resonant frequencies) of the sound.

The same logic applies to differences in vocal tract size and length. The vocal tract would be equivalent to the tube section of the different horns and is generally considered the area from the larynx to the front of the mouth (i.e., the lips and incisor teeth). Individuals with longer vocal tracts tend to produce sounds with lower frequency resonances, or formants, while those with shorter vocal tracts produce sounds with higher frequency resonances. This pattern is evidenced conspicuously in humans in the difference in voice timbre between adult men, women, and children.

The vocal tract can be further subdivided into two component sections. The oral component includes the area between the lips and the back of the throat, while the pharyngeal component includes the area beyond this that extends to the position of the larynx. In some species, the vocal tract does not contain a pharyngeal component or only a relatively small one because the larynx is situated high in the vocal tract near the posterior margin of the oral cavity. However, in some other species, there is a more developed pharyngeal cavity because the larynx sits relatively low in the vocal tract. Humans are a good example of this with a larynx that occupies a descended position in the vocal tract creating a large pharyngeal cavity that is posterior and caudal to the oral cavity.

1.2.3 Is Vocal Signaling of Body Size Honest?

If competition is mediated by body size, and body size is signaled vocally, then there should be reliable cues to a signaler's size contained in either the F_0 or F_n of their signals, or both. In fact, there is some supporting evidence but it is often mixed or weaker than expected. For example, there is a general pattern of age- and sex-related differences in the voice that track gross differences in body size in many species. Immature individuals tend to have higher voice pitch and resonances than adults, and adult females have higher voice pitch and resonances than adult males. In humans, listeners are sensitive to these differences and can use them to discriminate the age and sex of unseen speakers (e.g., Coleman, 1976; Smith & Patterson, 2005; Whiteside, 1998) and thus also make relative size inferences based on them. However, within age–sex classes the relationships are less clear. For example, in humans, there seems to be no consistent relationship between voice pitch, in particular, and body size within either men or women (e.g., Collins, 2000; van Dommelen & Moxness, 1995; Gonzalez, 2004; Kunzel, 1989; Rendall, Kollias, Ney, & Lloyd, 2005; but see also Evans, Neave, & Wakelin, 2006). Overall, the bulk of past research shows weak or little evidence of a consistent relationship between F_0 and body size within age-sex classes.

1.2.4 Resonants as Better Cues to Body Size

In view of the lack of clear relationships between voice F_0 and body size, Fitch (1997) proposed that the resonant frequencies of vocalizations might provide more accurate cues to body size. His reasoning is that F_n are a direct consequence of the length of the vocal tract, which, in turn, should correlate better with overall body size than the vocal folds (Fitch, 2000b).

There is some evidence in support of Fitch's hypothesis (1997), but, once again, the evidence is mixed and often weak or inconsistent. For example, a number of studies have demonstrated significant relationships between body size and either vocal tract length or the resonant frequencies of vocalizations. However, once again, many studies have involved collapsing data across age and sex classes. Hence, they have confirmed that males of many species are larger than females (for reasons outlined earlier) and also produce vocalizations with lower F_n (Bennett, 1981; Fitch, 1997; Fitch & Giedd, 1999; Charlton, Zhang, & Snyder, 2009; Riede & Fitch, 1999). However, when analyses are done within particular age-sex classes, the relationships often break down entirely or are significant for only one sex and not the other (Charlton, Zhang, & Snyder, 2009; van Dommelen & Moxness, 1995; Rendall et al., 2005).

Age may also be an important confound to consider (Bruckert, Lienard, Lacroix, Kreutzer, & Leboucher, 2005; Fischer, Hammerschmidt, Cheney, & Seyfarth, 2002; Ey, Pfefferle, & Fischer, 2007) because, as individuals age, their bodies grow and so too does the length of the vocal tract. Hence, all else equal, older individuals will have longer vocal tracts and lower F_n than younger individuals. Taken together, failing to control for inherent variation in F_n due to age and sex-related variation in body size risks creating a distorted picture of the extent to which F_n cues to body size may be reliable within any particular age-sex class where the relevant pressures of sexual selection are occurring.

1.3 The Perception of F_0 and F_n Cues to Body Size

An important corollary of the possibility that animals mediate competition by means of vocalizations that reliably advertise body size is that perceivers must be able to detect and accurately interpret such vocal cues. There is also a substantial literature on this topic that, once again, involves a mix of outcomes.

1.3.1 Perception of F_0 Cues to Body Size

Although the bulk of work suggests that the F_0 cues available in vocal signals are often not very reliable predictors of body size within age-sex classes, many perceptual studies nevertheless find that listeners attend to F_0 cues and attempt to use them to gauge the body size of signalers (van Dommelen, 1993; Gonzalez, 2003; Rendall, Vokey, & Nemeth, 2007; Smith & Patterson, 2005). Further, when more reliable F_n cues to body size are juxtaposed with the inherently less reliable cues provided by F_0, listeners appear to rely primarily on the F_0 cues when judging size (Rendall et al., 2007). Why listeners do this is unclear but the effect may be due, in part, to the role of F_0 in reliably signaling sex-based differences between males and females, including body size differences.

F_0 is affected to a large extent by the length of the vocal folds, as outlined earlier. However, F_0 is also affected by circulating hormones because the vocal folds contain a host of androgen receptors. Consequently, F_0 may serve as a reliable indicator of masculinity (qua testosterone). Several studies confirm that listeners use variation in voice F_0 when judging the sex and attractiveness of speakers. When voice F_0 is experimentally lowered, the speaker is rated as more masculine and attractive if their F_0

falls within the frequency range typical of males; but male speakers are rated as more feminine and less attractive if their F_0 falls within the frequency range typical of females (Pisanski & Rendall, 2011). Hence, listeners use of F_0 as a cue to body size, where it is relatively unreliable, might arise in part because it is a reliable cue of masculinity, which in turn may be interpreted as a proxy for large body size, at least in a between-sex context as reviewed earlier.

1.3.2 Perception of Resonance Cues to Body Size

In general, resonant frequencies appear to be a more reliable cue to body size than fundamental frequency. However, research testing the perceptual salience to listeners of more reliable F_n cues to body size has yielded mixed results. Some studies suggest that people and non-human animals are able to employ F_n to estimate the size of a speaker (Charlton, Reby, & McComb, 2007; van Dommelen & Moxness, 1995; Feinberg, Jones, Little, Burt, & Perrett, 2005; Fitch, 2000d; Taylor, Reby, & McComb, 2011). While other studies suggest that this ability is limited and is clearest only when the naturally confounding cues to size provided by F_0 cues are experimentally controlled or minimized (Rendall et al., 2007).

1.4 Implications for human language

These issues of reliable body size signaling and its vocal anatomical bases also bear importantly on another more specific and long-standing problem in the evolution of communication, namely the origins and evolution of language. The connection lies in the enigmatic origins of human language and the extent to which it is or is not intimately linked to unique features of human vocal anatomy.

The origins and evolution of language are an active area of research but prove difficult problems to solve because language leaves few fossil traces. However, one important line of argument traces the origins of language to the descended position of the larynx in the vocal tract of humans compared to its relatively high position in our primate ancestors (Lieberman, 1969, 1993). Indeed, the larynx of a human adult is descended in the vocal tract to such a large degree that the length of the pharyngeal cavity nearly matches the length of the oral cavity. In most other species, including our closest living relative the Common Chimpanzee, the larynx is located near the back of the oral cavity with little or no discernible pharyngeal cavity. And this lack of a significant pharyngeal cavity is considered a primary reason why non-human animals do not have vocal language abilities (Lieberman, 1969, 1993).

1.4.1 The Phonetic Expansion Hypothesis of Laryngeal Descent

Lieberman (1969) argued that the descended position of the larynx in humans was key to the emergence of articulate language because it created a large pharyngeal cavity, in addition to the oral cavity common to other animals. This development, along with a pliable tongue, allows for the production of a wider range of resonant patterns through dynamic modification of vocal tract articulators that alter the size and shape of the oral and pharyngeal cavities. It is precisely this wider array of resonant patterns that define the many different vowels that make up contemporary language systems. Hence, the descended larynx is regarded as a keystone adaptation in generating the sound diversity that underscores complex language in humans.

This hypothesis is wholly reasonable on the surface of it. However, it faces a growing number of challenges, not least of which is an explanation of the selective processes that might have initiated the descent of the larynx. Originally, Lieberman (1993) proposed that the incremental descent of the larynx would lead to correlated incremental increases in the individual's phonetic abilities. However, research by Boe et al. (2007) suggests that the kind of linguistic benefits Lieberman argues derive from a descended larynx would only accrue after the larynx had descended a considerable degree. Unless one assumes that the human larynx descended 'all at once', it is not clear what pressures initiated the process of laryngeal descent before there were any appreciable linguistic benefits.

At the same time, recent research shows that a descended larynx is not a uniquely human trait. In fact, it characterizes a variety of nonhuman and nonlinguistic species. For example, in European Red Deer, the larynx occupies a permanently descended position relative to related species and it is also subject to additional dynamic descent during vocalization (Fitch & Reby, 2001; Reby & McComb, 2003). The result is a vocal tract of approximately 75 centimeters while the Red Deer is vocalizing. Similar phenomena have been described for Koalas (Charlton et al., 2011), some species of cats (Weissgruber, Forstenpointner, Peters, Kubber-Heiss, & Fitch, 2002), and Elephant Seals (Sanvito, Galimberti, & Miller, 2007). Hence, a descended larynx, by itself, is no longer considered a necessary requisite for language.

1.5 Alternatives to the Phonetic Expansion Hypothesis

1.5.1 Body Size Exaggeration

Fitch (1997) proposed that resonant frequencies could serve as reliable cues to signaler size. But once perceivers utilize F_n as a cue to body size, Fitch suggested that a potential benefit arises for those that are able to vocally *exaggerate* their size (Krebs &

Dawkins, 1984; Fitch, 2010). One means to accomplish such size exaggeration would be through dynamic or permanent lowering of the larynx, creating a longer vocal tract with lower resonant frequencies that produces an acoustic impression of larger body size.

Of course, such deceptive size signaling through ever-increasing laryngeal descent must eventually confront the limits of anatomy. The larynx can descend only so far and then honesty is restored to the signaling system, in which the largest individuals once again have the longest vocal tracts and manifest the lowest F_n (Fitch 1997; 2010). Indeed, this process is observed in European Red Deer where dynamic descent of the larynx reaches the physical boundary of the sternum (Fitch & Reby, 2001).

Fitch has offered this “Size Exaggeration Hypothesis” as an alternative to Lieberman’s (1969, 1993) Phonetic Expansion hypothesis for laryngeal descent in humans (Fitch, 1997, 2000, 2010). Although the Size Exaggeration Hypothesis is also intuitive on the surface, it confronts the problem of receiver skepticism. As noted by Maynard-Smith (2004), an individual may be able to gain some short-term term advantage in mate competition and mate access by making himself appear larger through deceptively low-frequency vocalizations accompanying a descended larynx. However, that individual’s actual physical competitive ability has not been materially changed by the deception and all parties to such competitive interactions are under selection to act adaptively. Hence, one expects that selection operating on receivers favors individuals that begin to discount and ignore the altered vocalizations of competitors or potential mates so as to avoid being duped and suffering continuing fitness costs.

1.5.2 Laryngeal Descent Accompanying Cranio-Facial Remodeling

A second alternative to account for laryngeal descent in humans is that it represented, at least in the initial stages, an integrated response to selection on other aspects of cranio-facial anatomy in evolving humans. In addition to a modified laryngeal position, humans are distinct from non-human primate ancestors in having a much more globular skull (neurocranium) reflecting a dramatic increase in brain size over the course of human evolution and also a flatter facial profile reflecting a substantial reduction in facial prognathism from ape and early hominin ancestors (Lieberman, 2008). The results of such cranio-facial remodeling are twofold, a dramatic reduction in oral cavity length and also a compacting of the skull base region arising from flexion of the skull base in response to neurocranial expansion. Either or both pressures may have started the process of laryngeal descent to compensate for the shrinking of the vocal tract's oral cavity. Put differently, if there were not some compensatory descent of the larynx, the vocal tract of evolving humans would have become very short and disrupted previously adapted systems of vocal production and perception already in place to support important aspects of social communication (Ghazanfar & Rendall, 2008).

In support of this possibility, Laitman and Reidenberg (1988) found a relationship between the shape of the basicranium (in particular the Cranial Base Angle) and the structure of the vocal anatomy. When the basioccipital bone of the cranial base was surgically lowered, the position of the larynx was also lowered. Hence, it seems possible that the incremental enlargement of the brain in evolving humans and the corresponding enlargement of the basicranium and shrinking of the facial structures, may have forced the larynx away from the base of the skull, explaining at least the initial stages of laryngeal descent.

This hypothesis is difficult to test directly because the laryngeal complex is composed of cartilaginous tissues that do not fossilize well (Fitch, 2000); hence, it is difficult to establish with certainty the position of the larynx in the vocal tract of different hominin species (e.g., see Boe et al. (2002) and Lieberman (2007) for debate on laryngeal position in Neanderthals). However, indirect tests may be possible using other species for which laryngeal position can be established confidently and compared in cases where selection has produced cranio-facial modifications analogous to those that characterized human evolution.

1.6 Outline of Thesis

The remainder of this thesis contains two empirical chapters specifically designed to examine important issues in the two previously presented alternatives to the Phonetic Expansion Hypothesis. Both Fitch's Body Size Exaggeration Hypothesis and the hypothesis based around cranio-facial re-modeling address the same phenomenon, the descended position of the larynx in humans. However, neither of these alternative theories have been properly tested; therefore, the research presented here is designed to analyze important issues in laryngeal descent by focusing both on size signaling and on the effects of cranio-facial form. Chapter 2 attempts a direct test of Fitch's hypothesis that resonant frequencies should provide reliable cues to body size via their connection to overall vocal tract length. The hypothesis is tested using morphometric data collected from two different canine species: the Portuguese Water Dog and Russian Silver Fox. For both species, the data involve direct measures of body size and measures of vocal tract length obtained from radiographic images of the upper body and head. Chapter 3 provides an indirect test of the hypothesis that laryngeal descent in humans may have been due, at least in part, to changes in cranio-facial anatomy. The hypothesis is tested using the Portuguese Water Dog sample which includes individuals exemplifying cranio-facial variation analogous to the cranial and facial size and shape modifications that occurred in human evolution. This sample is studied for evidence that laryngeal position in the dogs is sensitive to changes in cranio-facial size and shape as hypothesized for evolving hominins. Finally, Chapter 4 reviews the major findings and conclusions and considers some potential shortcomings of the work and possible future directions.

Chapter 2

Radiographic Analysis of Vocal Tract Length and its Relation to Overall Body Size in Two Canid Species

2.1 Introduction

Body size is a general feature of organismal biology with broad behavioral significance. In many species, successful competition for food, other resources or mating opportunities is determined in part by body size. For example, in many mammals, larger bodied males can physically dominate rivals to monopolize access to female mates, and are sometimes also preferred as mates by females. Thus, larger size in males can be favored by both inter- and intra-sexual selection pressures, often resulting in extreme sexual dimorphism in size (reviewed in Fairbairn, Blanckenhorn, & Székely, 2007).

As direct physical confrontation can be dangerous, it is expected that organisms will develop methods of indirectly signaling their size and competitive ability as an alternative to direct confrontation. Distinctive vocalizations are often a central part of inter- and intra-sexual selection displays. Males of many species produce loud vocalizations when competing aggressively with rival males or when courting females (e.g., baboons: Fischer et al., 2002; Pfefferle & Fischer, 2006; elephant seals: Sanvito et al., 2007; red deer: Fitch & Reby, 2001). These vocal signals play a functional role in intimidating rivals and attracting females by providing honest, or exaggerated, acoustic cues to body size. Listening males and females may use acoustic cues to assess the caller's threat as a competitor or their appeal as a potential mate (e.g., Reby & McComb, 2003; Reby et al., 2005; Charlton, Reby & McComb, 2007; Taylor, Reby, & McComb, 2010). As a result, a central focus of animal communication research and theorizing is the extent to which animal vocal signals convey honest cues to body size (Fitch, 1997; Searcy & Nowicki, 2005).

While a variety of voice features could be involved in cueing body size, research to date has focused on two core elements of voice production and their acoustic consequences: 1) voice fundamental frequency (F_0), or pitch, which is attributable to the rate of vibration of the vocal folds of the larynx; and 2) voice resonances (F_n), which are attributable to the filtering action of the cavities of the vocal tract.

Voice pitch often differs consistently between males and females, as well as between adults and juveniles. These sex and age contrasts also correlate with substantial differences in body size (e.g., Inoue, 1988; Titze, 1989; Hammerschmidt & Fischer, 1998; Fischer et al., 2002; Hammerschmidt et al., 2000; Rendall et al., 2004). Hence, there is a general correlation between voice pitch and body size across age-sex classes. Older individuals have lower-pitched voices than younger individuals, and, within adults, males have lower-pitched voices than females. However, within age-sex classes, such as within adult males, or within adult females, the correlation between voice F_0 and body size is not so reliable (Kunzel, 1989; Hauser, 1993; Masataka, 1994; van Dommelen & Moxness, 1995; Appleby & Redpath, 1997; Fitch, 2000; Rendall et al., 2005; Pfefferle & Fischer, 2006; Riede, Arcadi, & Owren, 2007; Evans, Neave, Wakelin, & Hamilton, 2008; Frey & Riede, 2013).

The general unreliability of voice pitch as a cue to body size within age-sex classes may be due, in part, to the fact that normative voice pitch is determined by mechanical properties of the vocal fold tissues (Chan, Fu, Young, & Tirgunagari, 2007; Riede & Titze, 2008; Riede 2010; Riede et al., 2010; Titze, 2011). Vocal fold tissue properties, in turn, are influenced by circulating hormones and these may vary considerably between individuals independently of differences in body size between them (Goldman & Salmon, 1942; Beckford, Rood, Schaid, & Schanbacher, 1985; Jenkins, 1998; Dabbs & Mallinger, 1999; Evans et al., 2008). Thus, at the level that is most relevant to adjudicating aggressive mate competition and mate choice, that is between adults of both sexes, cues to body size derived from voice pitch are often not very reliable.

In view of this complication, a second and more recent focus of research has been on voice resonances. Following the source-filter theory of human voice production (Fant, 1960), voice resonances are a straightforward consequence of the length and cross-sectional area of the vocal tract (see Taylor & Reby (2010) for a recent review of the application of source filter theory to animal signals). Building on this logic, Fitch (1997) proposed that voice resonances could be a reliable source of cues to body size, particularly more reliable than voice pitch. This hypothesis proposes that voice resonances provide honest cues to body size because they are determined by the length of the vocal tract, which, in turn, scales predictably with overall body size (see Figure 2.1). The pattern of voice resonances should therefore be an honest cue to a signaler's overall size.

There have been a number of tests of Fitch’s hypothesis that have involved a variety of species, mostly but not exclusively mammals. A selection of studies and their main results are summarized in Table 2.1. A majority of studies have focused on the relationship between body size and the pattern of voice resonances. Overall, the results of such studies have been generally supportive but they have sometimes also involved mixed or weak outcomes. For example, in the first studies, Fitch (1997) reported a very strong correlation between voice resonances, or formants, and body size in rhesus monkeys, while Riede and Fitch (1999) reported similarly strong correlations between voice resonances and body size in domestic dogs. Subsequent studies of other species, including humans, baboons, red deer, elephant seals, giant pandas, as well as frogs and toads, also reported correlations between voice resonances (or dominant frequency) and signaler body size (see Table 2.1). However, in some of these latter studies, the relationship between voice resonances and body size was relatively weak or even non-existent. For example, von Dommelen and Moxness (1995), Bruckert et al. (2005), and Rendall et al. (2005) all reported relatively weak correlations between voice acoustics and body size in humans, and no significant relationships at all for one or the other sex. Likewise, Charlton et al. (2009) reported a relationship between voice resonances and body weight in male giant pandas but not in females.

At the same time, many of the studies reporting very strong correlations have involved small samples, or samples that involved a very heterogeneous mix of subjects. For example, Fitch (1997) was based on only 20 rhesus monkeys that ranged in age from 1 to 9 years and involved both males and females. As a result, the very strong correlations reported between voice resonances and body size for this sample involved collapsing the data across age-sex classes. The results, therefore, confirm well-established differences in body size and voice acoustics between adults and juveniles and between males and females, as outlined earlier, but they do not test whether the correlation between voice resonances and body size also holds within any of these age-sex classes, particularly within adults where the hypothesized sexual selection pressures would apply.

Similarly, the study by Riede and Fitch (1999) involved a large sample of dogs (n=47) but included individuals from 21 different breeds ranging from some of the smallest breeds available (e.g., Dachshund, Pekingese and Shih tzu) to some of the largest (e.g., German Shepard, Dobermann and Rottweiler). The dogs spanned more than an order of magnitude in body mass (from 2.5 kg up to 50 kg) and they also ranged in age from juveniles (0.5 years) to very old individuals (15 years). As a result, the strong correlations between voice acoustics and body size in this sample confirm extensive breed differences in these traits, but they do not speak to whether body size variation is correlated with voice acoustics within any one breed. Pfefferle and Fischer (2006) involves a similar sampling confound in using a sample of only 13 baboons of markedly different ages (1-28 years old) and both sexes (1 adult male, 7 adult females).

Sampling confounds like these also complicate the interpretation of the few more challenging studies that have tried to directly address the relationship between body size and vocal tract length directly. Fitch and Giedd (1999) undertook a unique MRI study of humans to get direct measures of vocal tract length and they reported very strong correlations between the length of the human vocal tract and body size, measured in terms of height and weight. Here again, though, the sample was extremely heterogeneous, involving both males and females ranging in age from 2 to 25 years. Analyses were performed only on the data collapsed across all age ranges and across both sexes. The strong correlations that were obtained thus confirm important basic developmental differences in human body size and vocal tract anatomy as people mature from infancy through adulthood. As humans grow from babies to adults, they get bigger (taller and heavier) and their vocal tracts get longer. Unfortunately, analyses were not performed within age-sex classes, perhaps possibly because the sample sizes within age-sex classes were relatively small. So, it remains unclear whether the more subtle differences in body size that occur within adult males or within adult females are also matched by subtle differences in vocal tract length within men and women as predicted by Fitch's hypothesis.

The only other study we are aware of directly addressing the relationship between vocal tract length and body size is Riede and Fitch (1999), mentioned previously. That study involved X-ray measures of vocal tract length in domestic dogs in addition to measures of body size and voice acoustics. However, as noted earlier, this work involved a critical confound in its use of a very wide range of dog breeds spanning more than an order of magnitude in body weight. Hence, here too it is not clear whether modest differences in body size within adult males (or adult females) of a particular breed, for example Rottweilers, are matched by correlated differences in vocal tract length.

Overall, then, the logic of Fitch's hypothesis of voice-based body size cueing is compelling and there is some supportive evidence. To date, that evidence concerns primarily only acoustic studies comparing the pattern of voice resonances with some metric of body size (either height, length or weight), and, as just reviewed, the relationships reported have often either been weaker than expected or complicated by sampling confounds. To date, there is no evidence confirming the more direct relationship between the length of the vocal tract and overall body size when the sample is not confounded by variation in age, sex, or breed. In this chapter, we attempt to fill the latter gap using unique radiographic samples of a large number of adult males and females belonging to two different canid species. The goal is to systematically test for correlated variation in vocal tract length and body size in a large sample where age- and sex-variation are controlled, thereby allowing a direct and cleaner test of Fitch's hypothesis.

2.2 Materials and Methods

2.2.1 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* (PWD). PWD's were originally bred and utilized by fisherman in the Portuguese fishing fleet (Chase, Adler, Miller-Stebbings, & Lark, 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 descendant individuals from the founder population is known across 26 subsequent 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; Chase et al., 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 and generally in a standardized position, with a quarter placed on the imaging table to allow size standardization. The radiographic sample involved 547 individuals. However, many individuals 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 taken, and we feared that the wide-diameter tubing 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 (greater than 2 years).

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 based on their temperament as a means of investigating the process of domestication (Trut, 2001; Trut et al., 2006; Kharlamova, Trut, Chase, Kukekova, & Lark, 2010; Kukekova et al, 2011). Imaging was done in the parasagittal plane and standardized for all individuals. For each individual, two radiographic images were made, one from each side. The sample involved a nearly balanced set of 64 females and 57 males.

2.2.2 Anatomical Measures

Multiple measures of body size were made previously and described in Chase et al. (2002). Based on that analysis, we selected the length of two long bones (femur and humerus) as good metrics of size. We did not use body weight because of possible idiosyncratic differences among individuals in diet, activity, condition, and fat as observed in other domestic species (e.g., Rendall et al., 2005).

To obtain accurate 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 anterior (or rostral) boundary of the oral component was defined to be the tips of the upper incisors, which were clearly visible on all images. The posterior 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 tempero-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 posterior (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 posterior boundary were subsequently labeled as VTL_H and measures of overall vocal tract length based on the cricoid as the posterior boundary were subsequently labeled VTL_C. Sample radiographs of a PWD and fox are shown in Figures 2.2 and 2.3 with labels illustrating the vocal tract landmarks and the distances between them that were used to generate measures of overall vocal tract length and of the lengths of the oral and pharyngeal components of the vocal tract. 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) and recorded in number of pixels. To evaluate measurement reliability, 10 images were randomly selected for remeasurement of each vocal tract dimension with a different set of 10 images selected for each dimension. This procedure involved remeasuring approximately 10% of the sample. The difference between original and remeasured values was generally very low, averaging 3.42 pixels (s.d.= 4.75) or 1.76%, indicating very good measurement reliability.

2.2.3 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 (Figure 2.4). 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, Franklin, Lane, Temaine, & Allen, 2008). To evaluate and control for possible effects due to variable head extension, we also measured the angle between a line connecting bulla to incisors and a second line through the vertebral canal for each individual (Figure 2.2). 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 by the visibility of both the left and the right bulla in some x-ray 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.

2.3 Results

2.3.1 General Body Size and Vocal Tract Characteristics

Descriptive statistics for body size and vocal tract characteristics for the two species are provided in Tables 2.2 and 2.3, and trait correlations are given in Tables 2.4 and 2.5. For both species, there was significant sexual dimorphism in body size and vocal tract dimensions, with males being larger than females. Dimorphism values were consistent and similar for all traits and both species, with males being 5-7% larger than females. The only deviations from this pattern concerned two vocal tract dimensions in the fox sample (Hyoid-Bulla and Cricoid-Bulla) where dimorphism values were nearly doubled to 11%.

Trait correlations were consistent and similar in the two species and for both sexes. In both PWD and fox samples, the two body size traits (femur and humerus length) were significantly and strongly correlated with each other in both males and females (r=0.72-0.90), as were the two measures of overall vocal tract length (VTL_H and VTL_C; r=0.84-0.96). Both measures of vocal tract length were also significantly correlated with both measures of body size for males and females, 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 in both sexes, but the magnitude of the correlations was larger between the two pharyngeal component measures (Hyoid-Bulla and Cricoid-Bulla; r=0.52-0.79) than between either of these measures and the single oral component measure (Bulla-Incisor; r=0.26-0.37). Measures of the constituent components of the vocal tract correlated variably and sometimes non-significantly with the two measures of body size. For example, Bulla-Incisor was significantly and strongly correlated with both femur and humerus length in both species (r=0.41-0.75), while the correlation of Hyoid-Bulla and Cricoid-Bulla with these body size measures was relatively weak (r=0.28-0.58) and often not significant for one or the other sex and sometimes both.

2.3.2 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, s.d.=13.8; Females: M=121.7, s.d.=14.2), while for the fox sample this angle ranged from 56-94 degrees (Males: M=71.1, s.d.=7.5; Females: M=77.8, s.d.=7.0). In separate bivariate regressions, this angle significantly affected measures of Hyoid-Bulla and Cricoid-Bulla for males and Hyoid-Bulla for females in the PWD sample, and significantly affected measures of Bulla-Incisor in the female fox sample (see Table 2.2 and 2.3 for statistics), although in no case did Head Position explain more than 11% of the variation in these vocal tract dimensions. Effects were nearly significant for measures of Cricoid-Bulla and VTL_H for females in the fox sample, but the effects were not significant for the remaining vocal tract dimensions.

To generate unbiased measures of vocal tract dimensions for further analyses of their relationships with overall body size, we used the residuals from these bivariate regressions. As a precaution, we undertook this procedure for all vocal tract dimensions, not just those significantly affected by head position.

2.3.3 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 employing humerus and femur length as independent variables. Results are shown in Figures 2.5 and 2.6 as well as Tables 2.6 and 2.7. The outcomes were very similar for both sexes and across the two species for overall vocal tract length. 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 53% of their variation, respectively. 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 (Bulla-Incisor), explaining 33% and 54% of its variation in males and females, respectively (see Table 2.6 for statistics). However, body size did not significantly influence the length of either measure of the pharyngeal component of the vocal tract (Hyoid-Bulla or Cricoid-Bulla).

In contrast, in the fox sample, body size had more consistently significant effects on the length of the constituent components of the vocal tract (see Table 2.7 for statistics). Body size significantly influenced the oral component (Bulla-Incisor) in both males and females, and also both pharyngeal components (Hyoid-Bulla and Cricoid-

Bulla) in males and one of these (Cricoid-Bulla) in females, explaining between 12% and 34% of the variation in these dimensions.

2.4 Discussion

Our results show a consistent and positive relationship between body size, assessed by long bone length, and the length of the vocal tract in adult males and adult females of two canid species. This is an important finding. Although a correspondence between vocal tract length and broader body dimensions is intuitive and well justified on theoretical grounds (Fitch, 1997; Fitch, 2010), empirical tests of the relationships have often yielded mixed results and been plagued by critical confounds. 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 (e.g., infants versus adults; males versus females). However, prior work has not clearly established that vocal tract length necessarily tracks the much smaller degree of variation in body size that occurs among individuals within any of these age-sex classes. Here, our results are important in showing that vocal tract length does track body size variation in large samples of adults of two species where, for both samples, age- and sex-related variation in vocal tract and body size dimensions were controlled. These results are some of the clearest evidence to date in support of Fitch's proposal that the vocalizations of animals might generally provide accurate cues to body size via the effects of size-related variation in vocal tract length on voice acoustics.

It is important to note that the size-related effects we observed were stronger for some components of the vocal tract compared to others. In both the PWD and fox samples, the oral component of the vocal tract was strongly influenced by body size (*qua* long bone length). However, the effects were much weaker and less consistent for the pharyngeal component. In the PWD sample, there was no significant influence of body size on the length of the pharyngeal component of the vocal tract in either males or females. In the fox sample, the effects for the pharyngeal component were relatively weak and less consistently significant compared to those for the oral component. These outcomes suggest that there might be some independence in the growth of the oral and pharygneal components of the vocal tract (Vorperian et al., 2009, 2011) and that asymmetry may account for previously reported mixed results.

Some independence in the growth of the oral and pharyngeal components of the vocal tract may be due to differential physiological or developmental constraints. The oral component of the vocal tract is completely surrounded by, and indeed in some sense is defined by, the bony anatomy of the face and skull. Hence, the size of the oral component of the vocal tract is effectively determined by the growth and size of the face and skull and will track variation in overall body size to the extent that cranio-facial growth programs do. In contrast, the length of the pharyngeal component of the vocal tract is determined primarily by the height of the larynx, as the larynx defines the caudal boundary of the vocal tract. The height of the larynx (and thus the length of the pharyngeal component of the vocal tract) may often be more free to vary independently of body size because it is not as systematically defined by, or rigidly attached to, surrounding bony anatomy.

The resting position of the larynx is influenced by the anatomy of pharyngeal and extrinsic laryngeal musculature and the hyoid skeleton. The ability to move the larynx during vocalization depends on the flexibility of these structures. For example, the ligamentous connection between the larynx and the hyoid skeleton allows for dramatic dynamic descent of the larynx in European red deer during vocalization but only relatively modest descent in its American relative, the elk (Frey & Riede, 2013). Evidence from a variety of other species further confirms the potential for either dynamic, or permanent, descent of the larynx in the vocal tract (Fitch & Giedd, 1999; Fitch & Reby, 2001; Weissengruber et al., 2002; Nishimura, Mikami, Suzuki, & Matsuzawa, 2003; Sanvito et al., 2007; Frey & Riede, 2013).

This asymmetry in the potential constraints on size-related variation in oral versus pharyngeal components of the vocal tract might help to account for some of the mixed or weak size-related results reported previously in the literature. For example, there have been several previous studies of the relationship between vocal tract length, or voice acoustics, and body size in humans. The results have been mixed for many reasons already noted. For studies that have focused within a particular age-sex class, such as within adult males or within adult females, the results have generally been positive but weak: vocal tract length, or more often voice acoustic properties, have been positively but weakly related to variation in adult body size (Howard & Young, 1998; Griesbach, 1999; Gonzalez, 2004; Rendall et al., 2004; Bruckert et al., 2005). Past interpretations of these outcomes have varied. Some authors have emphasized the positive nature of the relationship, and interpreted it as confirmation of Fitch's hypothesis that voice acoustics accurately cue signaler body size; while others have emphasized that the relationship is surprisingly weak given the logic of the hypothesis and have thus questioned why voice acoustics are not, in fact, much more strongly correlated with body size.

However, if there can be some independence in the growth and size of the oral and pharyngeal components of the vocal tract, then in fact the two outcomes and interpretations can be reconciled. Measures of overall vocal tract length, or measures of voice acoustics that reflect the filtering effects of the entire vocal tract, may correlate with measures of body size, but the correlations might often be weak because the oral and pharyngeal components of the vocal tract are not equally well correlated with overall body size. Hence, the uncorrelated effects of one component of the vocal tract will then blur (and necessarily weaken) correlations due to the other.

This asymmetry in the extent to which the oral and pharyngeal components of the vocal tract track overall body size bears on an additional important point related to Fitch’s hypothesis of voice-based body size signaling, namely that it is open to deception. As Fitch himself has emphasized, the relative emancipation of laryngeal position in the vocal tract opens the door to deceptive body size signaling (Fitch, 1999, 2000, 2010). Organisms that can lower their larynx, either dynamically during vocalization, as in red deer 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; Fitch & Giedd, 1999; Riede & Fitch, 1999; Fitch, 2000b; Fitch & Reby, 2001). As a result, they can project in the reduced resonance frequencies of their vocalizations an exaggerated impression of their body size. Of course, such body size exaggeration may have physiological limits imposed by the anatomy of signalers (Fitch & Reby, 2001; Reby & McComb, 2003), or theoretical limits imposed by receiver skepticism (Maynard-Smith & Harper, 2004). Importantly, the potential for size deception in this way has been assumed to be grounded in the effects of variable laryngeal descent on overall vocal tract length.

Our findings highlight the possibility that it could reflect effects linked primarily to the pharyngeal component of the vocal tract, as this is the component of the vocal tract primarily affected by variable laryngeal position.

This straightforward inference arising from our results has two important implications for theory and research. First, the potential for honest and dishonest signaling of body size may exist simultaneously in many species. Acoustic cues emanating from the action of one component may provide relatively accurate cues to signaler body size, while acoustic cues emanating from the other component might not. Hence, it may 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 may often be both. The important corollary is that separating the oral versus pharyngeal contributions to the ultimate acoustic output of vocal signals might allow distinguishing the co-occurrence of honest and dishonest elements of body size signaling in a particular species. Accomplishing this will require a much better understanding of the detailed mechanics of vocal production than we currently have for most species in order to establish with confidence which aspects of the acoustic output reflect the action of the different components of the vocal tract. For example, in humans, we have some understanding of the spectral signatures of the front- versus back-cavity resonances in certain speech sounds (Stevens, 2000). However, we do not have anything like this kind of understanding for most other species.

Two final caveats bear emphasis. The first is that our results pertain only to the physical relationships between vocal tract dimensions and body size. They do not address the extent to which the actual vocalizations produced by either species studied necessarily preserve the physical relationships observed. In particular, it is possible that the position of the larynx is different in active, behaving animals compared to the anaesthetized animals studied, and further, that its position can be modified dynamically during vocal production. Such dynamic movement of the larynx has been reported previously for other dog breeds as well as several other mammals (Fitch, 2000b). Dynamic movement of the larynx while vocalizing would clearly alter the length of the pharyngeal component of the vocal tract and it might thus serve to further weaken the already weak and inconsistent relationships between pharyngeal cavity length and body size that we observed. Alternatively, laryngeal movement might actually serve to introduce a stronger relationship with body size and, in this way, increase or restore 'honesty' in the cueing of body size vis-à-vis the pharyngeal component of the vocal tract as well.

The second caveat to our results is that head position can affect measures of vocal tract length. This is particularly pronounced in the 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 by some degree. It is also unknown whether the degree of larynx elevation or lowering is a direct linear relationship with head extension/flexion or if some changes in head position affect larynx position to a greater extent than others. 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-à-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.

Our results confirm strong positive relationships between overall vocal tract length and linear metrics of body size within both adult males and adult females of two canid species. Because the size-related effects of age and sex were controlled in this study, these outcomes provide good support for Fitch's hypothesis of reliable signaling of body size via acoustic cues to vocal tract length. At the same time, our results highlight potential asymmetries in the extent to which the oral versus pharyngeal components of the vocal tract track variation in overall body size. Finally, our results underscore the impact that variable head and larynx positions may have both on measurements of vocal tract dimensions in anaesthetized animals and the extent to which the vocalizations ultimately produced by these animals preserve or distort the baseline physical relationships between vocal tract dimensions and body size.

Table 2.1: Summary of past studies of relationships between body size, vocal tract length, and voice resonances.

Author(s)	Species	Relationship*	Major Findings
Bruckert et al. (2005)	Humans	C [§]	No correlation between F_n and body size.
Charlton et al. (2009)	Giant pandas	C [†‡§]	Correlation between F_n and body weight in males but not females.
Fitch (1997)	Rhesus macaques	A, B, C [†‡§]	Correlation between body size, vocal tract length, and formant dispersion.
Fitch & Giedd (1999)	Humans	A [‡]	Correlations between height, weight and vocal tract length.
Fitch (2000c)	Primates and carnivores	A [‡§]	Correlation between weight and palate length.
Fitch & Reby (2001)	Red deer	B [†]	Correlation between vocal tract length and F_n.
Gonzalez (2004)	Humans	C	Weak relationship between body size and F_n.
Griesbach (1999)	Humans	C	Weak relationship between height and F_n.
Howard & Young (1998)	American toad	C [§]	Correlation between body size and dominant frequency in males.
Perry, Ohde, & Ashmead (2001)	Humans	C [†§]	Correlation between body size and F_n.
Peters, Baum, Peters, & Tonkin-Leyhausen (2009)	Various feline species	C [†§‖]	Correlation between body weight and mean dominant frequency.
Pfefferle & Fischer (2006)	Hamadryas baboon	C [†‡§]	Correlation between body size and formant dispersion.
Pfefferle, West, Grinnell, Packer, & Fischer (2007)	Lions	C [†§]	Correlation between chest circumference and F_n.
Reby & McComb (2003)	Red Deer	C [†§]	Correlation between body weight and lowest F_n.
Rendall et al. (2005)	Humans and baboons	C [†]	Correlation between height and F_n in males but not females.
Riede & Fitch (1999)	Domestic dogs	A, B, C [‡§]	Correlation between body mass, skull length

			and vocal tract length and formant dispersion.
Sanvito et al. (2007)	Elephant seals	A, B, C §	Correlation between body length and F_n.
van Dommelen & Moxness (1995)	Humans	A, C † §	No correlation between body size and F_n.
Wilczynski, Keddy-Hector, & Ryan (1992)	Cricket Frogs	C †	Correlation between body size and dominant frequency.

* Letters here represent specific relationships identified in Figure 2.1.
†= small sample size
‡= data collapsed across age-sex classes or across breeds or subspecies
§= other methodological issues (e.g., use of body weight as index of size; VTL estimated indirectly)

Table 2.2: Descriptive statistics and head position effects for Portuguese Water Dog sample.

	Mean* (Range)			T-test[†]	Head Position F-value and R^2 (p-value)	
Measurement	Male	Female	M:F Dimorphism	t-value (p-value)	Male	Female
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-Bulla	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-Bulla	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)

*Mean and range values are given in number of pixels

[†] T-test for sex difference

Table 2.3: Descriptive statistics and head position effects for fox sample.

	Mean* (Range)			T-test†	Head Position F-value and R^2 (p-value)	
Measurement	Male	Female	M:F Dimorphism	t-value (p-value)	Male	Female
Humerus	341.2 (315-360)	318.7 (298-335)	1.07	t= -13.85 ($p \leq 0.001$)	N/A	N/A
Femur	320.2 (300-337)	303.3 (278-321)	1.06	t= -12.38 ($p \leq 0.001$)	N/A	N/A
Bulla-Incisor	319.0 (302-340)	304.5 (291-319)	1.05	t= -12.99 ($p \leq 0.001$)	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 ($p \leq 0.001$)	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 ($p \leq 0.001$)	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 ($p \leq 0.001$)	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 ($p \leq 0.001$)	F= 0.49; R^2= 0.009 (p=0.488)	F= 0.35; R^2= 0.006 (p=0.559)

*Mean and range values are given in number of pixels

† T-test for sex difference

Table 2.4: 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
Bulla-Incisor	F M						
Hyoid-Bulla	F M	0.369* 0.369*					
Cricoid-Bulla	F M	0.256* 0.194	0.767** 0.788**				
VTL_H	F M	0.911** 0.932**	0.719** 0.680**	0.532** 0.460**			
VTL_C	F M	0.890** 0.880**	0.642** 0.676**	0.668** 0.637**	0.952** 0.955**		
Femur	F M	0.751** 0.413**	0.252 0.239	0.146 0.332*	0.673** 0.419**	0.653** 0.484**	
Humerus	F M	0.710** 0.572**	0.217 0.284*	0.180 0.306*	0.627** 0.561**	0.634** 0.593**	0.898** 0.722**
*$p \leq 0.05$; **$p \leq 0.001$							

Table 2.5: 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
Bulla-Incisor	F M						
Hyoid-Bulla	F M	0.116 0.347*					
Cricoid-Bulla	F M	-0.066 0.234	0.591** 0.586**				
VTL_H	F M	0.888** 0.918**	0.559** 0.692**	0.218 0.428**			
VTL_C	F M	0.732** 0.809**	0.494** 0.586**	0.631** 0.761**	0.839** 0.872**		
Femur	F M	0.588** 0.582**	0.063 0.385*	0.275* 0.530**	0.519** 0.612**	0.645** 0.710**	
Humerus	F M	0.569** 0.479**	0.209 0.440**	0.243 0.579**	0.572** 0.556**	0.608** 0.670**	0.797** 0.766**

*$p \leq 0.05$; **$p \leq 0.001$

Table 2.6: Results of multiple regression tests for effects of body size on overall vocal tract length and constituent components of vocal tract length for Portuguese Water Dog sample.

		Effects of Size*		
Vocal Tract Measure	Sex	*F-value*	*R^2*	*p*
VTL_H	M	11.87	0.294	$\leq$0.001
	F	20.62	0.420	$\leq$0.001
VTL_C	M	13.99	0.333	$\leq$0.001
	F	21.02	0.429	$\leq$0.001
Bulla-Incisor	M	13.81	0.326	$\leq$0.001
	F	33.53	0.541	$\leq$0.001
Hyoid-Bulla	M	2.29	0.074	0.111
	F	1.28	0.043	0.285
Cricoid-Bulla	M	2.34	0.077	0.106
	F	0.90	0.031	0.413
* Size is represented by humerus and femur length				

Table 2.7: Results of multiple regression tests of effects of body size on overall vocal tract length and constituent components of vocal tract length for fox sample.

		Effects of Size*		
Vocal Tract Measure	Sex	*F*-value	R^2	*p*
VTL_H	M	16.61	0.381	≤0.001
	F	12.40	0.289	≤0.001
VTL_C	M	29.94	0.526	≤0.001
	F	21.74	0.416	≤0.001
Bulla-Incisor	M	13.63	0.335	≤0.001
	F	13.71	0.310	≤0.001
Hyoid-Bulla	M	6.12	0.185	0.004
	F	2.45	0.074	0.095
Cricoid-Bulla	M	13.66	0.336	≤0.001
	F	4.26	0.123	0.019

* Size is represented by humerus and femur length

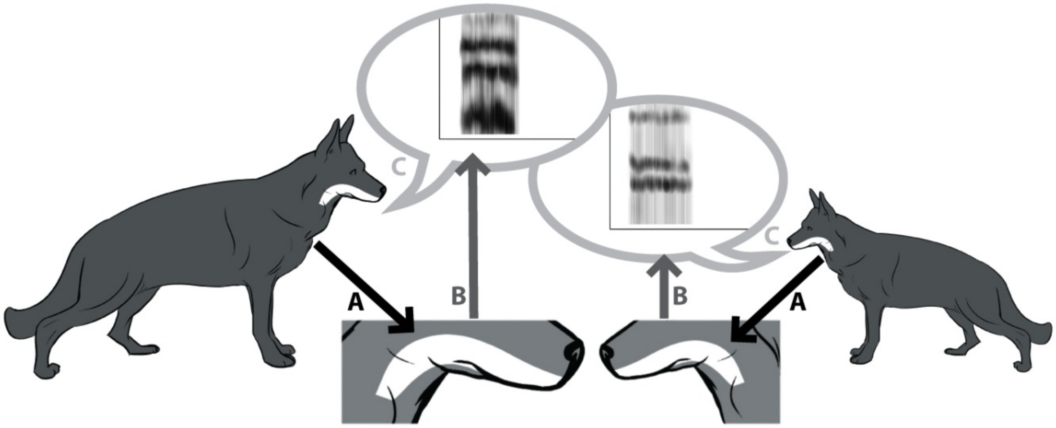

Figure 2.1. Schematic illustrating the various two-way relationships between overall body size, the length of the vocal tract, and the resulting pattern of voice acoustic resonances in two dogs of different size. The dog on the left is larger than the dog on the right and is therefore expected to have a longer vocal tract length and therefore also lower voice resonances. Past studies of these relationships have tended to focus on the relationship between overall body size and voice acoustics (relationship C) and relatively rarely on the relationship between overall body size and vocal tract length (relationship A), or the relationship between vocal tract length and voice acoustics (relationship B).

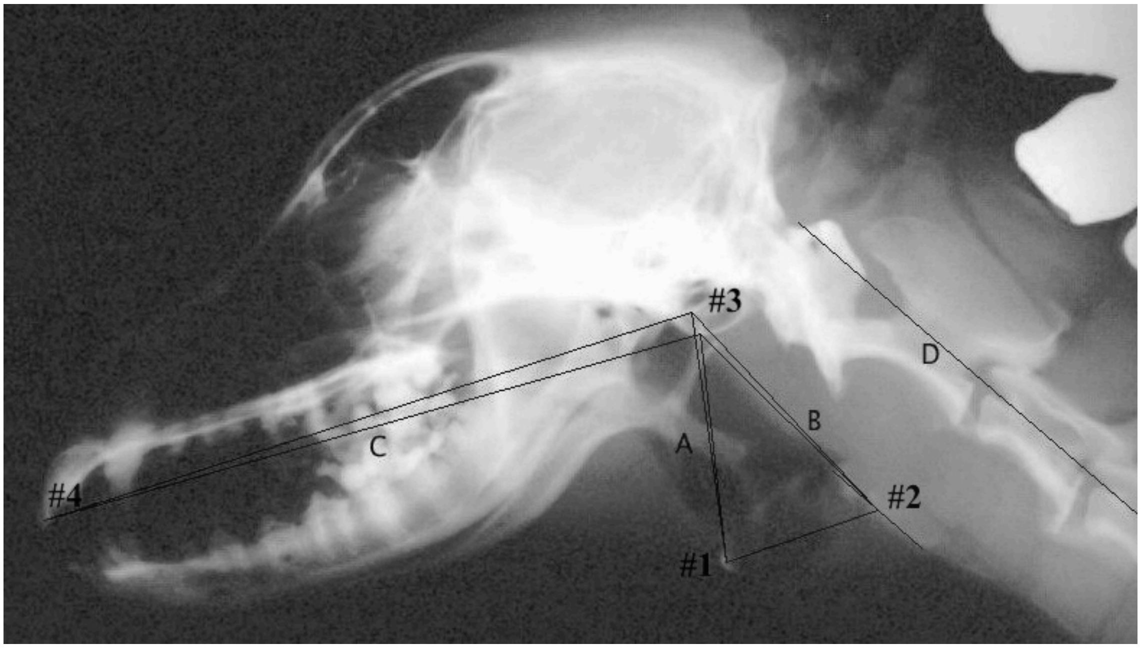

Figure 2.2. Radiograph of head and vocal tract of Portuguese Water Dog illustrating vocal tract landmarks and distances between them used to evaluate overall vocal tract length and the length of constituent components of the vocal tract. 1. Basihyoid; 2. Cricoid; 3. Bulla tympanica; 4. Incisors; A. Hyoid-Bulla distance; B. Cricoid-Bulla distance; C. Bulla-Incisor distance; D. Spinal axis.

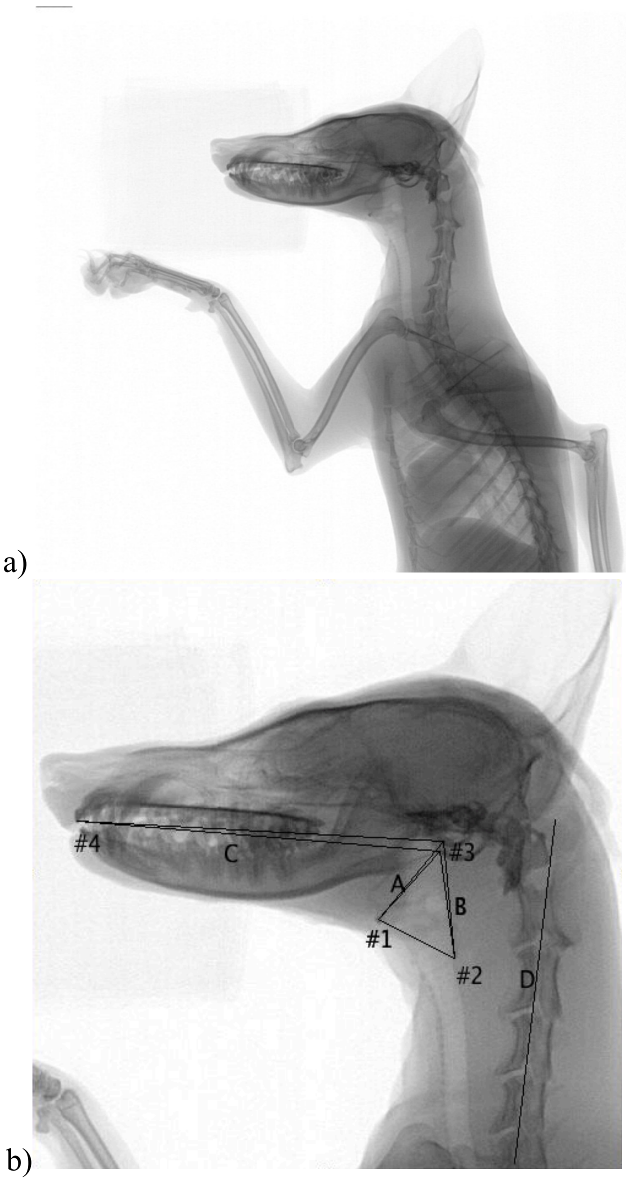

Figure 2.3. Radiographs of upper body (a) and head and vocal tract regions (b) of fox illustrating vocal tract landmarks and distances between them used to evaluate overall vocal tract length and the length of constituent components of the vocal tract. Landmarks and measurements are the same as those labeled in Figure 2.2.

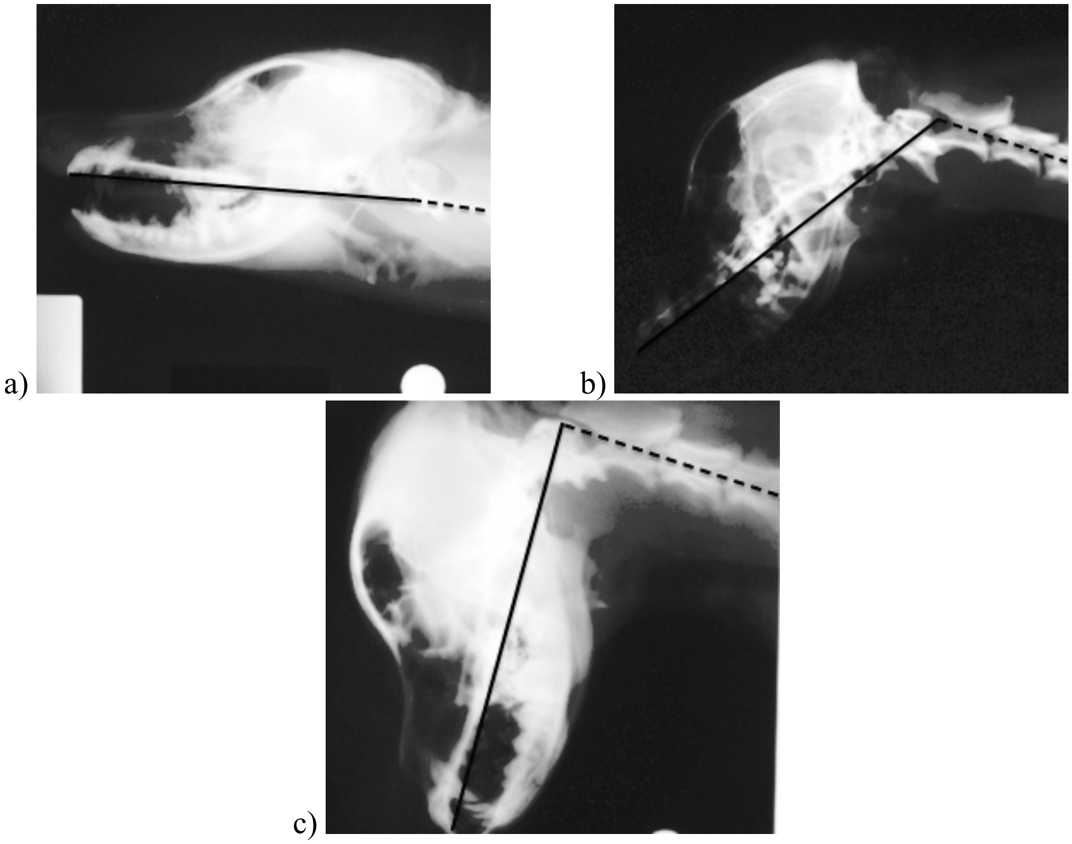

Figure 2.4. Radiograph images of Portuguese Water Dogs illustrating variation in the degree of head extension and flexion quantified as the angle of deviation from the spinal axis. a) 164°; b) 128°; c) 87°.

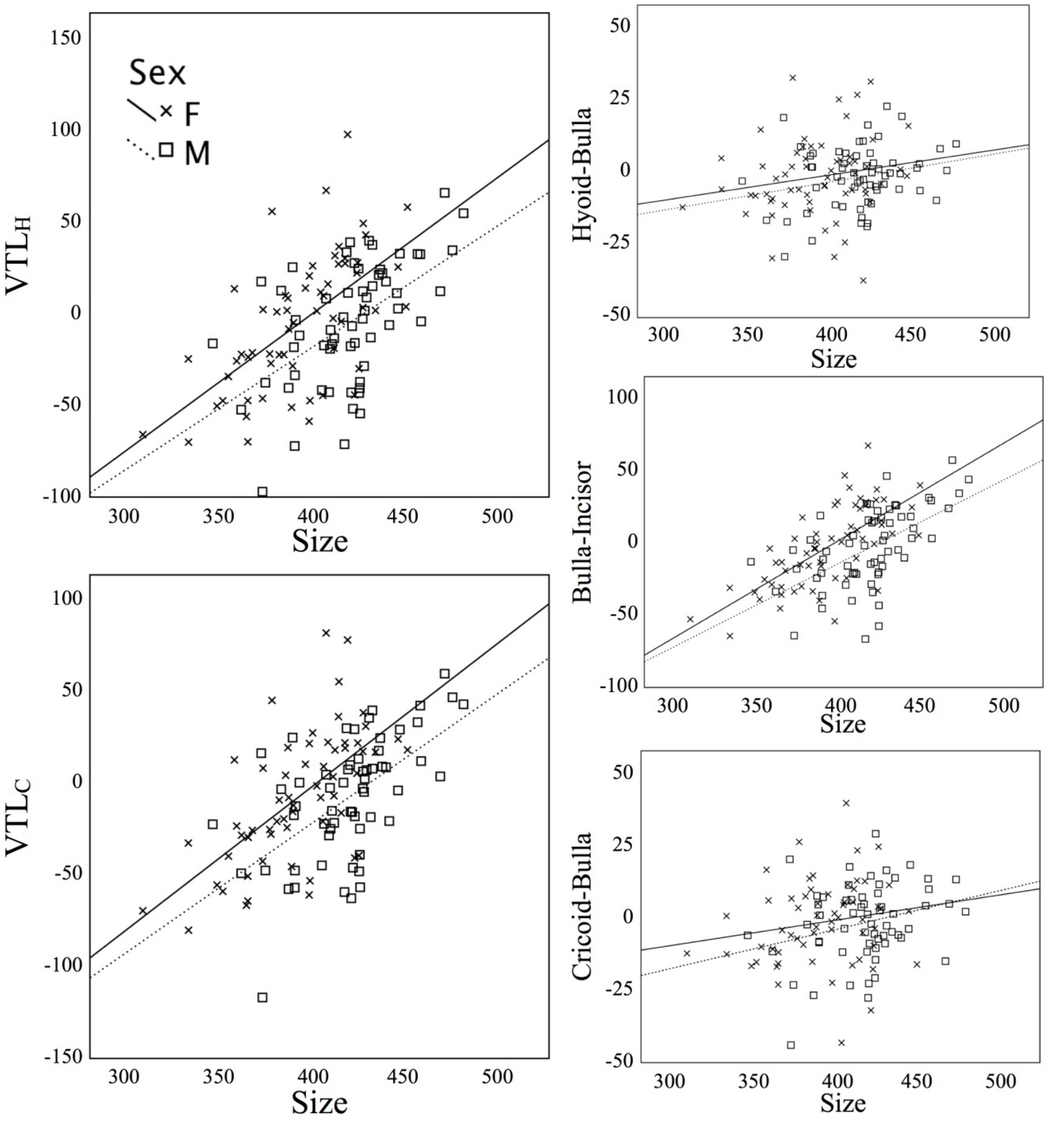

Figure 2.5. Relationships between body size (represented here by humerus length) and vocal tract length measurements in the Portuguese Water Dog sample. Vocal tract length measurements have been corrected for the effects of head position.

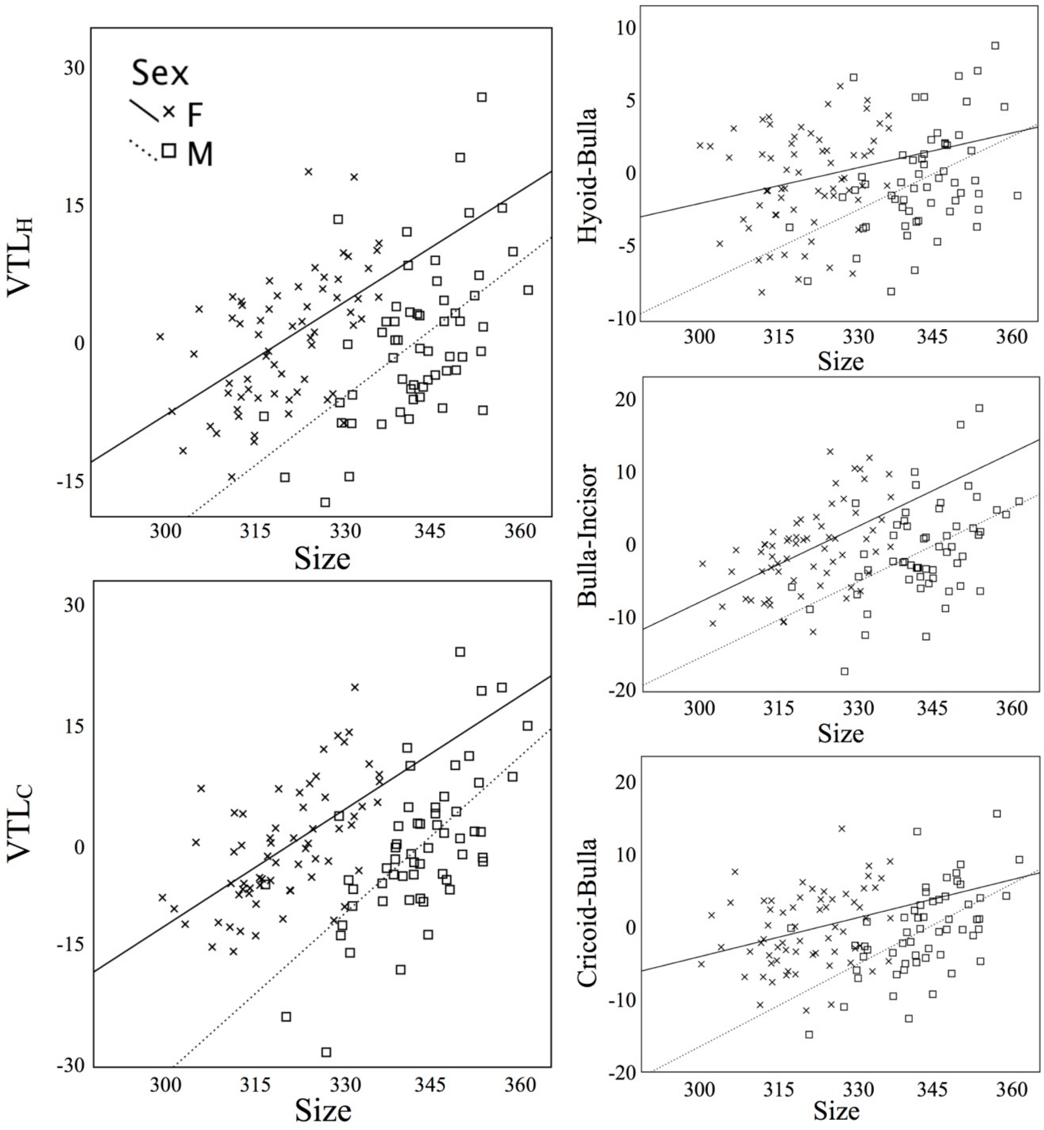

Figure 2.6. Relationships between body size (represented here by humerus length) and vocal tract length measurements in the fox sample. Vocal tract length measurements have been corrected for the effects of head position.

Chapter 3

Variable Laryngeal Position in Domestic Dogs in Response to Modified Cranio-Facial Dimensions and its Implications for Human Language Evolution

3.1 Introduction

The anatomy of the human vocal tract involves a descended position of the larynx relative to its position in the vocal tract of primate ancestors (Lieberman, 1969; Fitch, 2000). This descended larynx in humans is often attributed supreme importance in the evolution of language because it creates a more complex vocal tract configuration. In addition to the oral cavity common to non-human primates and other mammals, a descended larynx creates an additional, large pharyngeal cavity at the top of the throat extending caudally to the laryngeal body itself. This change in the size of the pharyngeal cavity is hypothesized to have spurred language by enabling the production of a much wider range of speech sounds, especially different vowel sounds (the Phonetic Expansion Hypothesis; Lieberman, 1969). The language and speech abilities of prehistoric humans are expected to have increased in conjunction with the descent of the larynx and these increased language abilities would then feedback and further drive the descent of the larynx to its current position in modern humans. Ultimately, then, the emergence of language in human prehistory, and its broader role in the evolution of complex societies and cultures, is thought to be traceable to the appearance of a descended larynx in the fossil record (Lieberman, 1993).

This is an intuitive proposal that enjoys some important empirical support (Lieberman, 1969; de Boer, 2010). However, the Phonetic Expansion Hypothesis has faced a growing number of problems and challenges. Because the larynx is composed of a mixture of cartilage, muscle, and bone, it does not fossilize as well as other areas of the skeleton that are composed of purely bone. Therefore, most proposals concerning the position of the larynx in ancestral fossils are inferential at best (Boe et al., 2002; Lieberman, 2007).

Furthermore, there is considerable debate concerning the amount of descent required to modify and improve speech abilities. It is possible that some of the hypothesized speech advantages of a descended larynx may not accrue until the larynx has already descended an appreciable distance (de Boer, 2010). If true, then some other pressure must be responsible for triggering the initial descent of the larynx. However, there is also research making the opposite point, namely that a descended larynx is not required to produce the majority of sounds employed in modern languages (Boe et al., 2007). Further, many languages make use of only a relatively small number of vowels and phonemes, and yet are perfectly functional (Maddieson, 1984). Hence, language itself might not have been a sufficient pressure sustaining incremental descent of the larynx to its current position.

A final concern is that the descended larynx is not unique to humans. Recent studies show that several non-linguistic animal species have either a permanently descended larynx or have a larynx that descends dynamically when they vocalize (Fitch & Reby, 2001; Reby & McComb, 2003; Weissengruber et al., 2002; Sanvito et al., 2007; Charlton et al., 2011). Consequently, there are factors other than language influencing laryngeal position and its permanent or dynamic descent in the vocal tract. Taken together, these problems suggest that a descended larynx and language may not be deterministically related; an alternative explanation seems to be necessary to explain the changes in human laryngeal position that occurred following our split from the last common ancestor with the great apes.

What has not been systematically considered previously is that laryngeal descent in humans may have arisen as a by-product of extensive remodeling of the skull and, in particular, the face during this period of human evolution. These alterations to the human face and skull occurred over an extended period of time in response to a variety of selective pressures (e.g., feeding, respiration, locomotion (Lieberman, 1993; Lieberman, 2008)). The end result was a significantly more globular neurocranium and a dramatically shorter face compared to primate ancestors. Without compensatory changes in laryngeal position, these dramatic changes in cranio-facial size and shape, particularly alterations in snout and oral cavity length, would have produced a dramatically shorter vocal tract; thereby potentially compromising co-evolved systems of vocal production and vocal perception that were already functional in the communication systems of early hominins.

Variants of this by-product hypothesis for laryngeal descent have been mooted before (Negus, 1949; Owren, 1996; Nishimura, Mikami, Suzuki, & Matzuzawa, 2006; Ghazanfar & Rendall 2008) but never systematically tested. It is, in fact, a difficult hypothesis to test directly because, as noted above, the human laryngeal complex does not fossilize well and hence its position in fossil material is difficult to establish or infer. However, the hypothesis can be tested indirectly by examining variable laryngeal descent in conjunction with changing cranio-facial shape in other species. Here, we provide such a test using Portuguese Water Dogs *(Canis lupus familiaris*; PWD*),* a breed of domestic dog originally bred and utilized by Portuguese fisherman (Chase et al., 1999). The breed experienced a catastrophic population decline and recovery in the last century and the current world stock is traceable to a founder population of 31 individuals. The PWD is the subject of a unique research program (the Georgie Project) that maintains a global database of all descendants of the founder population across 26 generations to facilitate genomic studies of morphological, physiological, and life-history traits (Chase et al., 2002; Chase et al., 2011). Notably, managed breeding of the dogs since their recovery has involved selection for different facial morphologies, specifically involving a long, narrow-faced (dolicocephalic) form and a comparatively short, broad-faced (brachycephalic) form. The differences between these two forms approximate the changes in cranio-facial form that occurred in human evolutionary history from relatively prognathic, long-faced ancestral species (e.g., Sahelanthropus sp.) to the relatively flat and broad facial profile of anatomically modern humans (H. s. sapiens). Hence, Portuguese Water Dogs offer a natural opportunity to test whether laryngeal position responds to global changes in cranio-facial size and shape.

3.2 Materials and Methods

3.2.1 Subjects

The sample involved radiographic images of the upper-body and head regions of a large sample of PWDs. 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 and generally in a standardized position, with a quarter placed on the imaging table to allow size standardization. The radiographic sample involved 547 individuals. However, many individuals 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 taken, and we feared that the wide-diameter tubing might distort natural vocal tract proportions. From the remaining sample of non-intubated dogs, we selected a balanced set of 55 individuals of each sex for the tracheal descent measurements. All individuals were adults (greater than 2 years).

3.2.2 Anatomical Measures

36 measures of skull features were made previously and described in Chase et al. (2002). To these measurements was added a measure of snout length, measured from the bulla tympanicus to the tip of the upper incisors (Bulla-Incisor distance). A Principal Component Analysis was used to reduce the large set of skull measures to a smaller number of orthogonal factors of size and shape variation.

Definitive identification of laryngeal position involved using the superior margin of the trachea as a key landmark identifiable in radiographs. The superior margin of the trachea corresponds to the posterior portion of the larynx and serves as an appropriate index of the most caudal position of the laryngeal body. The extent to which the larynx was descended in the vocal tract was evaluated by assessing its position relative to the body of the third vertebrae of the spine. For example, a value of 50% for laryngeal descent would correspond to a larynx whose most posterior margin was located mid-way along the body of the third vertebrae. A value of 100% would correspond to a larynx whose most posterior margin was located at the posterior margin of the third vertebral body. Recording and calculating these measurements involved a four-step process detailed in Figure 3.1.

All measurements were made using NIH Image (version 1.44o) and recorded in number of pixels.

3.2.3 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 along the sagittal plane (Figure 3.2). The degree to which head extension affects laryngeal position in sedated dogs 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 also measured the angle between the Bulla-Incisor line, described above, and a second line aligned with the vertebral column of each individual (See Figure 3.1). This angle quantifies the degree to which the head was extended away from, or flexed toward, the body in each image.

A second exception concerned the 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 naturally turn downward toward the table. This effect was made obvious in some x-ray images by the visibility of both the left and the right bulla tympanicus. To control for possible influences of an animal's head rotation on the Bulla-Incisor measurements, we measured from both the left and the right bulla to the front incisors and averaged the two measurements.

3.3 Results

3.3.1 Effects of Head Position on Larynx Position

In the sample, the angle between head and spinal axes ranged from 87-155 degrees in males (M=118.9, s.d.=13.8) and 85-164 degrees in Females (M=121.7, s.d.=14.2). In separate bivariate regressions, this angle significantly affected laryngeal descent measures in both males and females (Figure 3.3). Absolute head position explained 65% of the variance in male laryngeal descent and 34% of the variance in female laryngeal descent. To generate unbiased measures of laryngeal descent for further analyses, the unstandardized residuals from these bivariate regressions were utilized.

3.3.2 Principle Components Analysis

Using an eigenvalue cut-off criterion of 1, eight unrotated principal components (PCs) were derived for males and six principal components were derived for females. Collectively, these components explained 83.493% of the variation in male skull size and shape and 82.593% of the variation in female skull size and shape. In both sexes, PC 1 was strongly correlated with overall body size (males: $R^2= 0.341$; $p\leq 0.001$; females: $R^2= 0.810$; $p\leq 0.001$; Figure 3.4), indicating that it was capturing variation in overall skull size.

3.3.3 Variable Laryngeal Descent

To test the possibility that laryngeal position might vary with variation in face and skull size and shape, a stepwise multiple regression was conducted using the larynx position values (after correcting for head position) as the dependent variable and the PCs summarizing variable skull and shape as the independent variables. Regressions were run separately for each sex. This analysis revealed significant effects of face and skull dimensions on laryngeal position in both males and females. In males, the effects were attributable to PC4 (R^2= 0.086; p=0.029; Figure 3.5), which was associated with a set of 9 original face and skull variables (Table 3.3). For females, the effects were attributable to PC6 (R^2= 0.079; p= 0.045; Figure 3.7), which was associated with a set of 8 original face and skull variables (Table 3.4). These effects are illustrated in Figures 3.6 and 3.8.

3.4 Discussion

Results confirm that the largest proportion of variation in cranio-facial dimensions in PWD's was associated with differences in overall body size. This finding is entirely sensible in that the skull is comprised of boney structures whose growth programs are probably strongly related to developmental programs affecting bone growth generally and thus overall body size. Hence, larger-bodied individuals also have larger skulls.

More notably, results revealed significant effects of cranio-facial variation on larynx position. This effect seems likely to reflect selective breeding of PWD's specifically for different cranio-facial forms including a brachycephalic (broad-faced) form and a dolichocephalic (long-faced) form (K. Chase, personal communication). These findings deserve further scrutiny and interpretation in light of their potential implications for the hypothesis that laryngeal position in the human lineage was likewise affected by selection on variation in cranio-facial form.

In PWD's, laryngeal position in males was significantly affected by PC4 which was associated with several original variables capturing differences in the length and width of the face and skull. Key facial length variables were Mandible Length, Prosthion Length, Zygomatic Length, Internasal Length, and the Bulla-to-Incisor measure. In addition, Angle 1 was also implicated and positively associated with the other facial length variables, suggesting that the angle of the mid-facial ‘stop’ in PWD’s varies in conjunction with growth in facial length. Key facial width variables were Mandible Span, Snout Width, and both Upper and Lower Canine Span. In addition, Crest Length and Angle 3, which capture some of the variation in neurocranium size, were also implicated and positively associated with variation in facial width. Collectively, the set of variables significantly associated with variable laryngeal position in males is best characterized as a trade-off between facial length and width where facial shortening (and widening) was associated with increased laryngeal descent. This outcome is entirely consistent with the hypothesis that facial shortening and widening might similarly have affected laryngeal position in human evolution.

Laryngeal position in female PWD’s was significantly influenced by PC6, which was associated with several original variables related variously to midfacial regions and anterior and posterior regions of the face and skull. Key variables loading together on PC6 were Crest Length, Canine Span, Facial Height, Premaxilla and Angle 1. This set of variables is difficult to interpret simply but seems to describe dimensions of variation associated with anterior and posterior regions of the skull. Also loading together, but opposite to the other variables noted, were Zygomatic Length, Cranial Height, and Coronoid Span. Together, this set of variables described variation in the mid-facial region of the skull. It is difficult to infer a simple dimensional trade-off to explain this set of variables that were significantly associated with laryngeal position in females. However, one interpretation is that it represents a tradeoff between the size of anterior and posterior regions of the face and skull compared to mid-facial regions with greater larygneal descent associated with reduction in the front and rear of the face and skull.

Overall, these findings have important implications for the evolution of laryngeal descent in humans. They provide support for the hypothesis that changes in cranio-facial form occurring in the human lineage – specifically involving retraction and widening of the face and expansion of the neurocranium (Lieberman, 2008) – may similarly have been associated with changes in laryngeal position and favored increased laryngeal descent. The results for PWDs certainly confirm that laryngeal position is malleable in response to selection on variable cranio-facial form.

One explanation for the linked changes observed in laryngeal position and -facial form in PWD's (and possibly humans) could simply be that the developmental programs for laryngeal and cranio-facial anatomy are functionally integrated. Certainly, there is considerable evidence for integration of a broad array of other organismal systems (Wake & Roth, 1989). In this case, the critical functional needs of breathing, swallowing, and feeding might select for developmental integration of face, skull and connected laryngeal structures that must be coordinated in the service of these activities. Hence, laryngeal position may respond to changes in face and skull size in order to support continued coordinated functioning of all these structures to sustain of breathing, swallowing, and feeding abilities.

It is possible that functions associated with vocal communication also contribute to such integration. For example, in many primate species, the resonant frequencies, or formants, of vocalizations serve a variety of important social functions, including signaling an individual's body size (Fitch, 1997) or individual identity (Rendall, 2003). The primary determinant of the resonances of vocalizations is the length of the vocal tract (Fant, 1960; Fitch, 1997), and this, in turn, is determined by the length of the oral cavity and also the length of the pharyngeal cavity where present. Hence, an additional important functional factor promoting integration of laryngeal and cranial growth programs may be the need to maintain vocal tract length in the face of changes in cranio-facial form occurring for other functional reasons. Put differently, without correlated changes in larynx position, a reduction in facial length would be associated with a reduction in oral cavity length and thus overall vocal tract length. And this in turn would disrupt co-evolved systems of vocal production and perception based on the resonant characteristics of vocalizations produced. Hence, to maintain the utility of F_n in the species' communication system, the larynx may have descended to counterbalance the shortening of the snout, there-by preserving overall vocal tract length and the resonant frequency patterns produced.

Historically, the descent of the human larynx has been attributed to the production of language itself (the Phonetic Expansion Hypothesis: Lieberman, 1969), leading some researchers to argue that the position of the larynx in a fossil hominid is a good indicator of species' language abilities (Lieberman, 1969). There are a number of problems with this hypothesis, as outlined in the Introduction. However, the results presented here add further doubt in as much as they demonstrate that laryngeal position may respond to other functional pressures completely unrelated to language. If laryngeal descent can be associated with non-linguistic pressures, then the position of the larynx in ancestral humans can no longer be taken to be an indicator of language abilities, nor can it be taken to point to other complex human abilities (e.g., art, music, culture) that are often thought to be associated with the emergence of language.

Table 3.1: Legend detailing all measurements used and the location of landmarks for each measurement

Measurement	Location (Chase et al., 2002)	Section of Skull	Landmark 1	Landmark 2
Bulla to Incisor		Face Length	Bulla	Upper Incisor
Occipital Height	A1	Neurocranium	Bulla	Protuberentia occipitalis externa
Crest Height	A2	Neurocranium	Protuberentia occipitalis externa	Procesus tentoricus
Crest Length	A3	Neurocranium	Protuberentia occipitalis externa	Bregma= Suture line between frontal and occipal bone marking top/dorsal margin of sinus
Cranial Height	A4	Neurocranium	De ploe	Bulla
Skull Height	A5	Neurocranium	Bregma	Bulla
Skull Length	A6	Neurocranium and Face Length	Protuberentia occipitalis externa	Outside tip of the incisive bone (Prosthion)
Nasion	A7	Neurocranium and Face Length and Face Height	Infection point on slope of midface	Bulla
Internasal Length	A8	Basicranium and Face Length	Rostral end of Os nasale	Bulla
Prosthion	A9	Basicranium and Face Length	Processus alveolaris	Outside tip of the Incisive Bone
Zygomatic.Lv	A10	Basicranium and Face Length	Bulla	Back of 1st Molar
Coronoid Height	A11	Face Height	Top coronoid process of the mandible	Bottom of mandible
Mandible.Lv	A12	Face Length	Processus angularis	Lower Incisor 1: Processus alveolaris
Sinus and Orbit	A13	Face Height and Face Length	Inferior Orbit	Posterior Sinus
Sinus Length	A14	Face Length	Front Sinus	Rear Sinus
Sinus Height	A15	Face Height	Bottom Sinus	Top Sinus

Angle 1	A16	Face Height	Inflection point of top of skull/stop	
Angle 2	A17	Face Height	Inflection point on slope of midface	
Angle 3	A18	Face Height	Line: midline of os maxilla	Line: following 2nd part of Angle 2 above: inflection point on os frontalis
Facial Height	A19	Face Height	Inflection point on slope of midface	Ventral maxilla
Jugular	C3	Basicranium	Processus jugularus Left	Processus jugularus Right
Mastoid	C4	Basicranium and Neurocranium	Processus mastoides Left	Processus mastoides Right
Cranial Width	C5	Basicranium	Bulla	Bulla
Cranial Length	C6	Basicranium	Ventral margin foramen magnum	Dorsal end of Pterygoiedeum
Skull Width	C7	Basicranium and Face Width	Next to Process Zygomaticus Left	Next to Process Zygomaticus Right
Coronoid Span	C8	Face Width	Left mandible coronoid process	Right mandible coronoid process
Hamulus Span	C9	Basicranium and Face Width	Hamulus Pterygoiedeum Left	Hamulus Pterygoiedeum Right
Anterior Cranial Width	C10	Basicranium	Canalus alaris Left	Canalus alaris Right
Zygomatic	C11	Face Length	Anterior dimension of zygomatic arch	Posterior dimension of zygomatic arch
Mandible.1.L	C12	Face Length	Processus angularis	Lower Incisor 1: Prosthion: Processus alveolaris
Skull Base Length	C13	Basicranium and Face Length	Posterior margin of molars	Dorsal end of Pterygoiedeum
Mandible Span	C14	Face Width	Lower left 1st molar	Lower right 1st molar

Snout	C16	Face Width	Forament infraorbitale Left	Foramen infraorbitale Right
Upper Canine Span	C17	Face Width	Left upper canine	Right Upper Canine
Low Canine Span	C18	Face Width	Left lower canine	Right lower canine
Facial Length	C19	Face Length	Posterior margin of molars	Incisors
Premaxilla	C20	Face Length	Prosthion: Processus alveolaris	Posterior fissure palatine
Humerus		Body Size		
Femur		Body Size		

Table 3.2: Male and female principal components' eigenvalues and variation accounted for

Principal Component	Eigenvalues		Variation Accounted For (%)	
	Male	Female	Male	Female
PC1	16.516	20.839	44.637	56.321
PC2	3.563	3.323	9.631	8.980
PC3	3.283	2.449	8.872	6.618
PC4	2.472	1.573	6.682	4.251
PC5	1.507	1.376	4.073	3.718
PC6	1.348	1.134	3.642	3.065
PC7	1.197		3.234	
PC8	1.007		2.722	

Table 3.3: Principal components loadings for face and skull measures in sample of male PWD's.

Variable	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Bulla to Incisor	0.863	0.135	0.024	-0.296	-0.021	-0.169	-0.113	-0.078
Occipital Height	0.487	-0.417	-0.003	0.119	0.189	0.540	0.054	0.088
Crest Height	0.801	0.019	-0.235	0.060	-0.206	0.266	-0.076	-0.045
Crest Length	0.511	-0.011	0.341	**0.437**	0.127	0.180	-0.375	0.001
Cranial Height	0.274	-0.274	0.388	0.201	0.727	-0.127	-0.049	-0.073
Skull Height	0.708	-0.406	0.115	0.195	0.370	0.063	-0.052	-0.048
Skull Length	0.931	0.091	0.053	-0.219	-0.087	0.047	-0.056	0.042
Nasion	0.899	-0.153	0.008	-0.137	0.183	-0.220	0.120	-0.041
Internasal Length	0.839	0.222	0.126	-0.297	0.000	-0.156	-0.054	-0.098
Prosthion	0.871	0.173	0.098	**-0.328**	-0.034	-0.165	0.023	-0.113
Zygomatic.Lv	0.756	0.136	0.195	**-0.308**	0.048	-0.292	0.170	-0.244
Coronoid Height	0.760	0.024	0.144	-0.057	-0.215	0.308	-0.178	0.161
Mandible.Lv	0.817	0.113	-0.090	**-0.335**	-0.142	-0.037	-0.140	-0.058
Sinus and Orbit	0.703	-0.341	-0.203	-0.127	0.191	0.062	0.094	0.282
Sinus Length	0.605	-0.528	-0.223	-0.262	0.068	-0.089	0.245	0.147
Sinus Height	0.690	-0.316	-0.458	-0.191	-0.146	0.011	0.102	0.207
Angle 1	-0.145	0.431	0.573	**-0.313**	0.129	0.124	0.205	0.359
Angle 2	-0.211	0.540	0.516	-0.239	0.059	0.383	-0.029	-0.144
Angle 3	0.225	-0.453	-0.555	**0.399**	-0.130	-0.104	-0.134	-0.274
Facial Height	0.712	0.196	-0.257	0.094	-0.163	0.110	-0.303	0.088
Jugular	0.729	0.242	0.046	0.123	0.264	0.015	0.027	-0.127
Mastoid	0.817	-0.085	0.081	0.062	0.026	0.191	-0.066	-0.117
Cranial Width	0.717	-0.160	0.162	-0.014	-0.067	0.336	0.074	0.045
Cranial Length	0.516	-0.332	0.544	0.076	-0.061	0.020	0.173	-0.248
Skull Width	0.874	-0.018	0.057	0.142	-0.134	0.001	-0.163	0.004
Coronoid Span	0.769	-0.290	0.207	-0.053	-0.075	-0.016	-0.025	-0.131
Hamulus Span	0.304	0.070	0.229	0.294	-0.356	0.197	0.661	-0.114
Anterior Cranial Width	0.470	-0.562	-0.007	0.015	-0.056	-0.070	0.241	0.150
Zygomatic	0.797	0.289	-0.242	-0.195	0.017	0.000	-0.097	-0.081
Mandible.1.L	0.688	0.447	-0.394	0.091	0.176	0.081	0.161	-0.031
Skull Base Length	0.874	0.286	-0.104	-0.148	0.109	0.056	0.035	0.022
Mandible Span	0.554	0.401	0.074	**0.575**	-0.028	-0.074	0.184	-0.097
Snout	0.662	0.161	0.115	**0.544**	-0.235	-0.154	0.065	-0.058
Upper Canine Span	0.569	0.354	0.223	**0.462**	-0.086	-0.267	0.001	0.272
Low Canine Span	0.578	0.236	0.108	**0.348**	0.060	-0.274	-0.039	0.473
Facial Length	0.359	0.517	-0.668	0.087	0.240	0.089	0.158	0.060
Premaxilla	0.295	-0.406	0.633	-0.094	-0.332	-0.191	-0.181	0.157

Table 3.4: Principal components loadings for face and skull measures in sample of female PWDs.

Variable	PC1	PC2	PC3	PC4	PC5	PC6
Bulla to Incisor	0.888	-0.286	-0.059	0.073	-0.179	-0.105
Occipital Height	0.565	0.547	0.210	-0.293	-0.005	-0.116
Crest Height	0.791	0.177	-0.065	-0.140	-0.038	0.185
Crest Length	0.588	0.170	0.347	0.273	0.374	**0.442**
Cranial Height	0.468	0.281	0.484	0.105	0.447	**-0.324**
Skull Height	0.781	0.341	0.253	0.111	0.225	-0.180
Skull Length	0.949	-0.090	0.087	-0.118	-0.062	0.018
Nasion	0.937	-0.033	0.175	-0.040	0.063	-0.167
Internasal Length	0.919	-0.287	0.088	-0.027	-0.071	-0.112
Prosthion	0.918	-0.271	0.042	0.003	-0.055	-0.130
Zygomatic.Lv	0.788	-0.362	-0.017	0.015	-0.022	**-0.340**
Coronoid Height	0.865	-0.003	0.024	-0.060	0.070	0.183
Mandible.Lv	0.802	-0.336	-0.153	0.087	-0.135	-0.108
Sinus and Orbit	0.792	0.185	0.047	-0.422	-0.120	-0.080
Sinus Length	0.816	0.007	0.030	-0.336	-0.240	-0.189
Sinus Height	0.776	0.336	-0.129	-0.306	-0.253	-0.062
Angle 1	0.225	-0.583	0.507	-0.287	-0.123	**0.223**
Angle 2	0.046	-0.744	0.263	0.407	0.078	-0.182
Angle 3	-0.232	0.796	-0.326	0.022	-0.031	-0.068
Facial Height	0.736	0.035	-0.217	-0.008	-0.085	**0.250**
Jugular	0.841	-0.038	0.010	-0.087	0.140	0.110
Mastoid	0.914	0.049	0.106	-0.056	0.012	0.016
Cranial Width	0.874	0.144	0.126	0.205	-0.097	-0.040
Cranial Length	0.652	0.180	0.467	0.026	0.090	0.172
Skull Width	0.875	0.081	-0.139	0.265	0.037	-0.061
Coronoid Span	0.781	0.214	-0.035	0.156	0.178	**-0.237**
Hamulus Span	0.580	-0.054	-0.330	0.300	-0.299	-0.160
Anterior Cranial Width	0.586	0.493	0.152	0.153	-0.126	-0.032
Zygomatic	0.828	-0.196	0.003	-0.209	0.255	0.018
Mandible.1.L	0.757	-0.181	-0.408	-0225	0.320	0.053
Skull Base Length	0.939	-0.123	-0.096	-0.127	0.073	0.106
Mandible Span	0.705	0.113	-0.406	0.260	0.036	0.016
Snout	0.793	0.157	-0.295	0.323	0.053	0.097
Upper Canine Span	0.810	-0.018	-0.313	0.238	-0.109	0.160
Low Canine Span	0.829	-0.001	-0.044	0.086	-0.144	**0.300**
Facial Length	0.402	-0.350	-0.542	-0.230	0.434	0.087
Premaxilla	0.594	0.035	0.432	0.207	-0.417	**0.227**

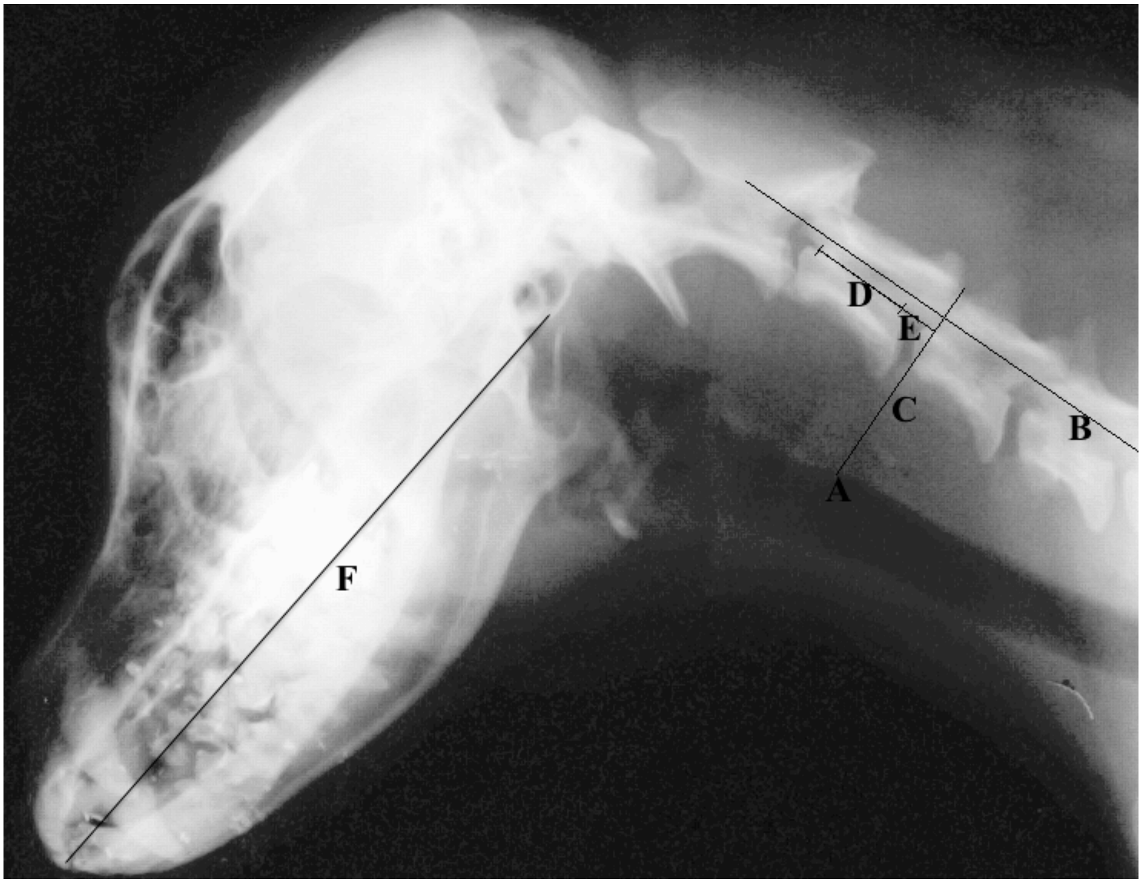

Figure 3.1. Radiograph of head and neck region of Portuguese Water Dog that illustrates the landmarks and measurements used to evaluate laryngeal descent. The first step was to identify the posterior margin of the larynx, which is coincident with the top of the trachea (point A). Next, a line was drawn through the vertebral column to delineate spinal angle (line B). A line was then drawn from the posterior margin of the larynx (point A) to meet line B at a perpendicular angle (line C). The degree of larynx descent is represented by where these two lines meet relative to the position of the third vertebral body. To quantify this position, a line was drawn along the extent of the third vertebral body to establish its length (line D). Then another line was drawn (line E) representing the distance from the anterior margin of the third vertebral body to line A. The length of line E relative to line A represents the proportional descent of the larynx with respective to the third vertebrae. The degree of head flexion or extension was established by computing the difference between spinal angle (line B) and snout angle (line F).

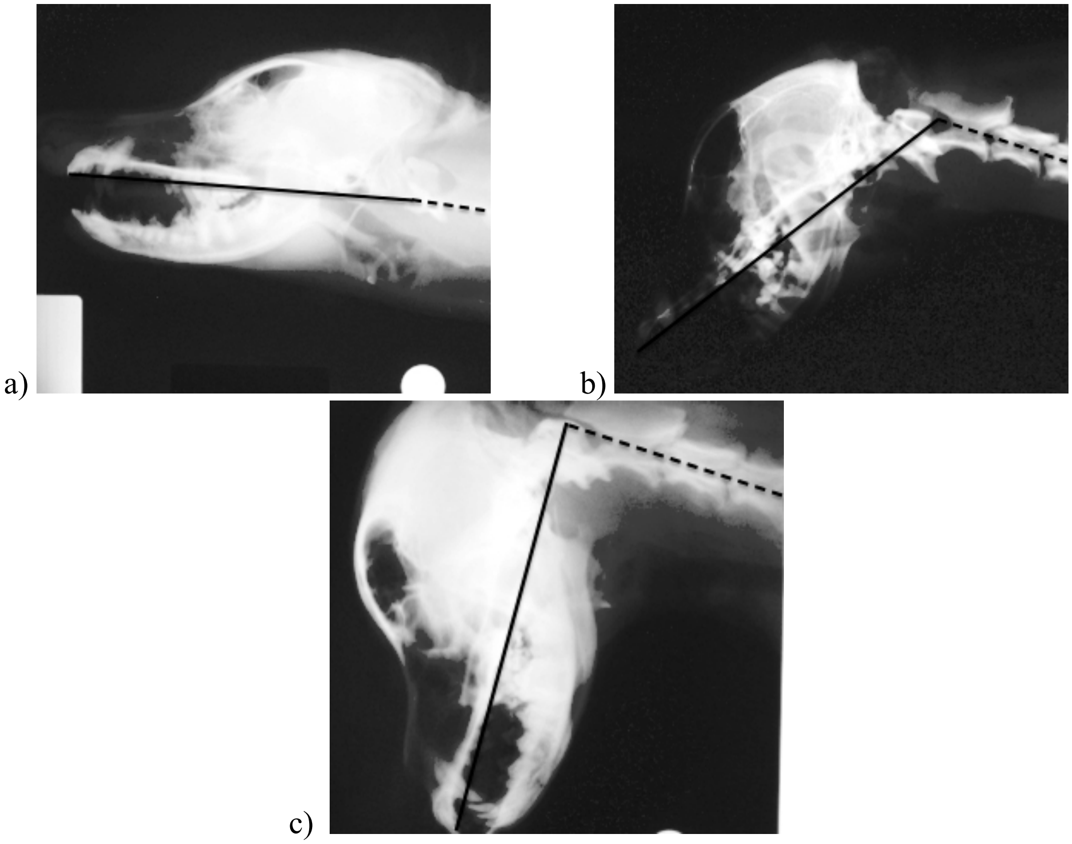

Figure 3.2. Radiograph images of Portuguese Water Dogs illustrating variation in the degree of head extension and flexion quantified as the angle of deviation from the spinal axis. A) 164°; B) 128°; C) 87°.

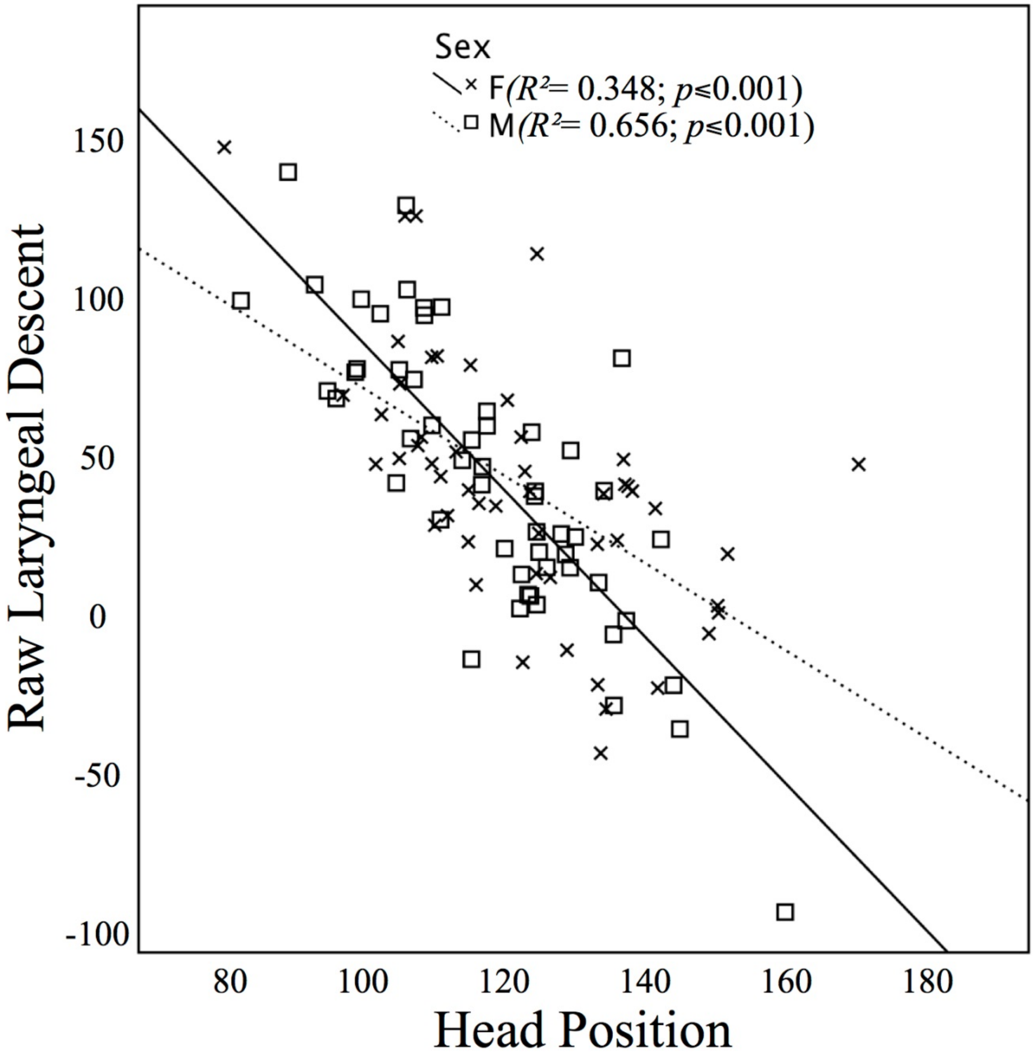

Figure 3.3. Head position plotted against absolute values of laryngeal position.

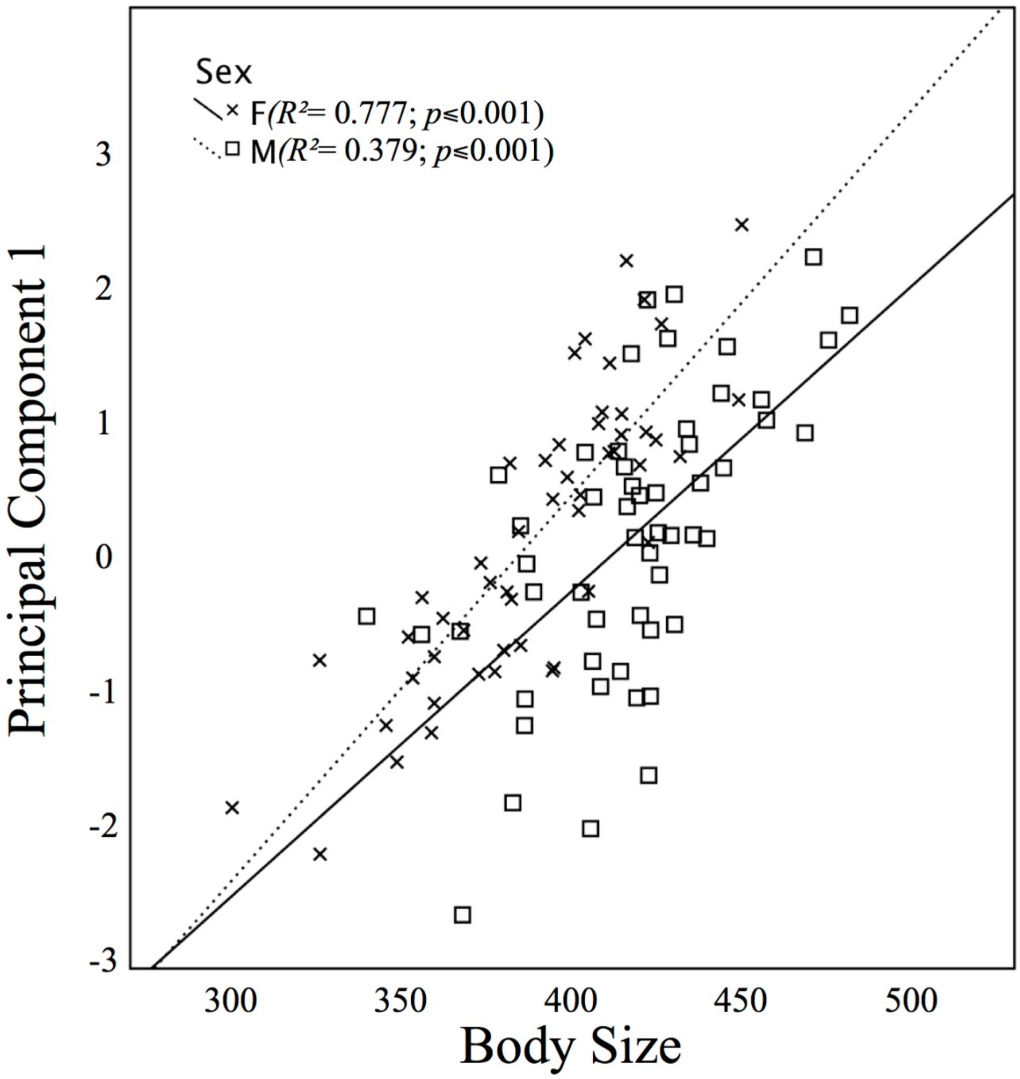

Figure 3.4. Graph showing the strong correlation between PC1 (summarizing variation in skull and facial variables) and body size (represented by humerus length) in both males and females.

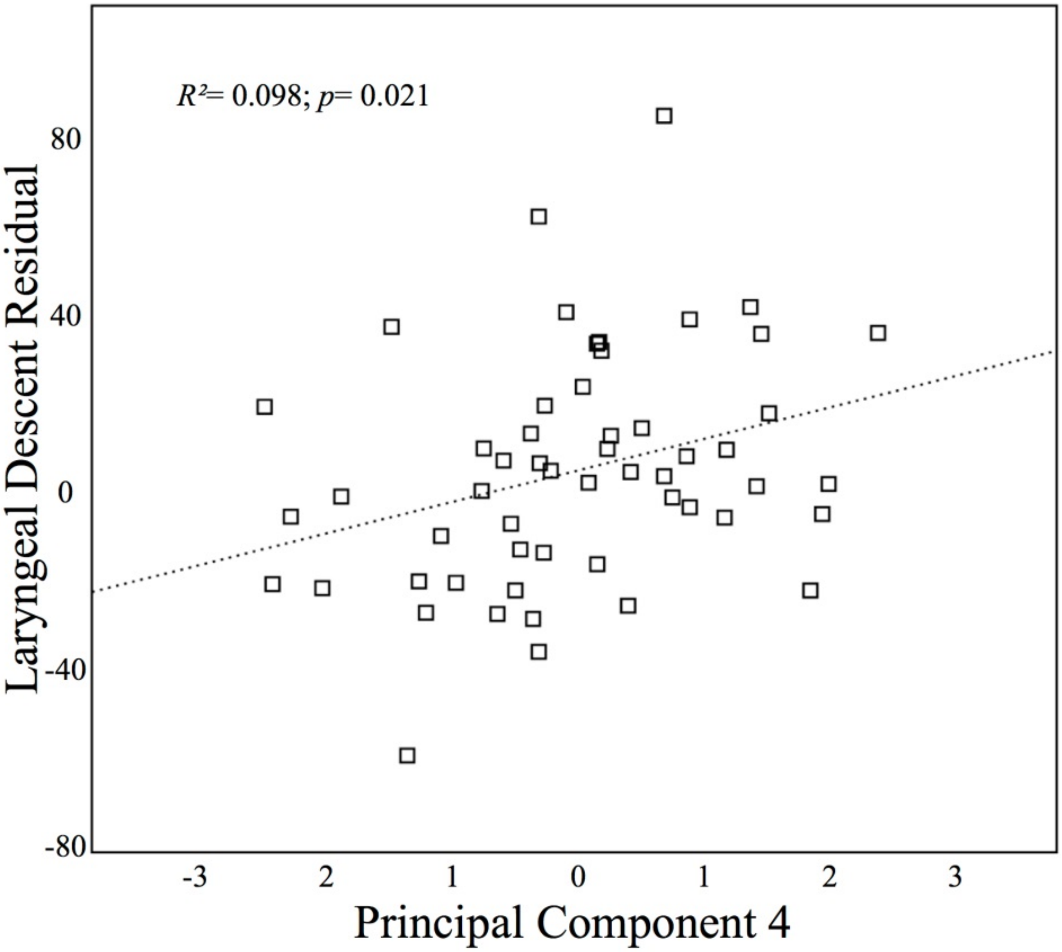

Figure 3.5. Graph showing the relationship between laryngeal position (after correcting for variable head extension or flexion) and PC4 in male PWD's.

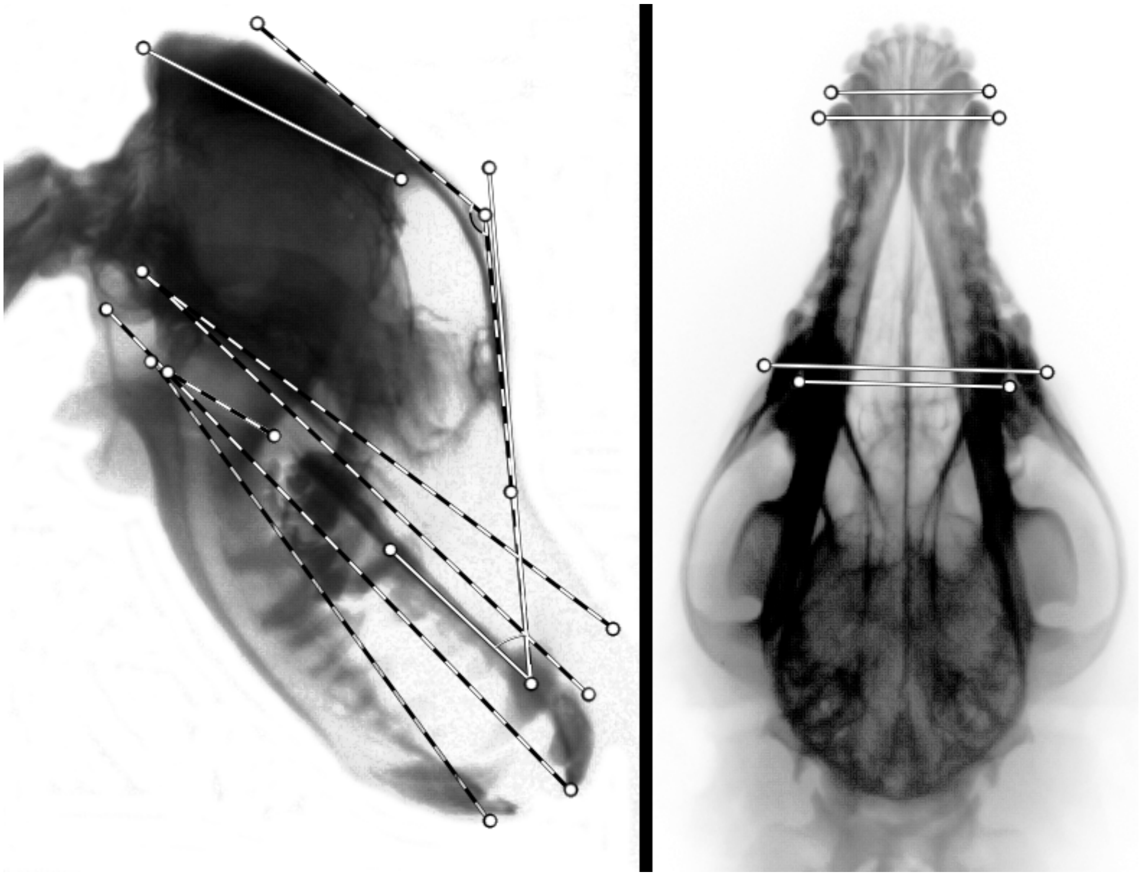

Figure 3.6. Lateral and dorsal radiograph images of male PWD skull highlighting skull and face variables varying significantly with laryngeal position. Solid lines and dotted lines indicate variables with opposing influences.

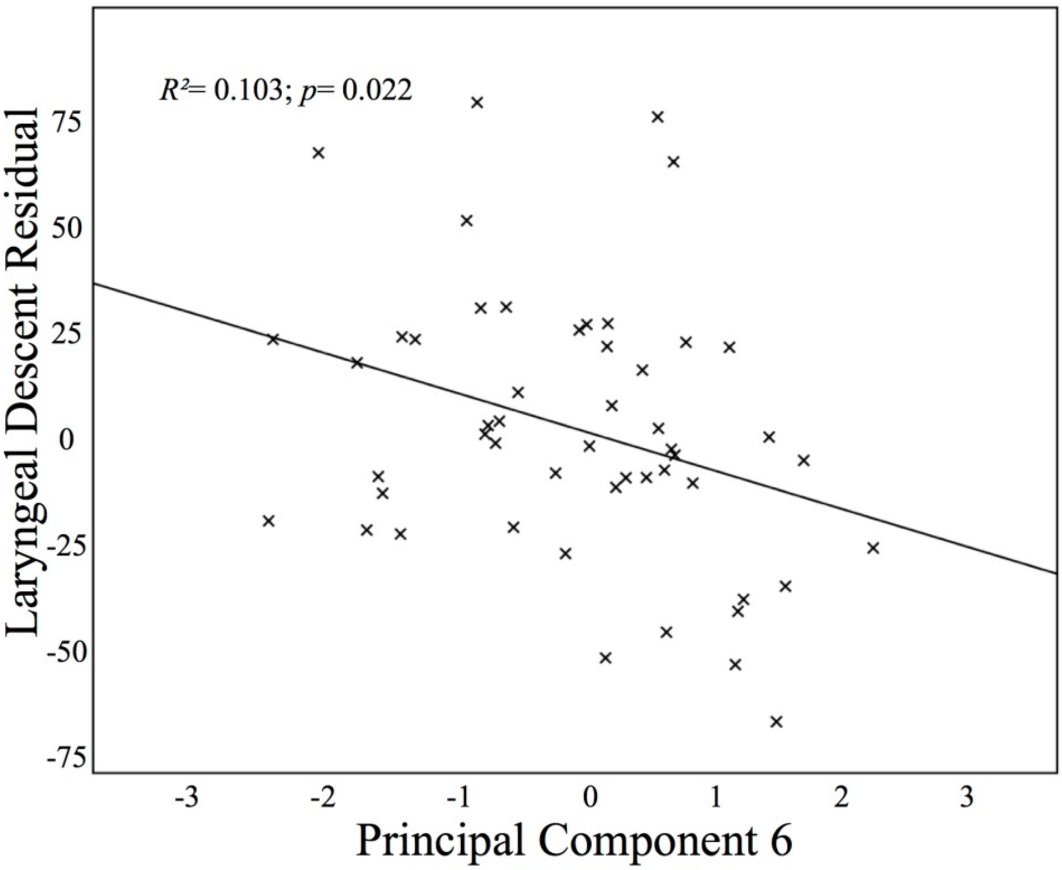

Figure 3.7. Graph showing the relationship between laryngeal position (after correcting for variable head extension or flexion) and PC6 in female PWDs.

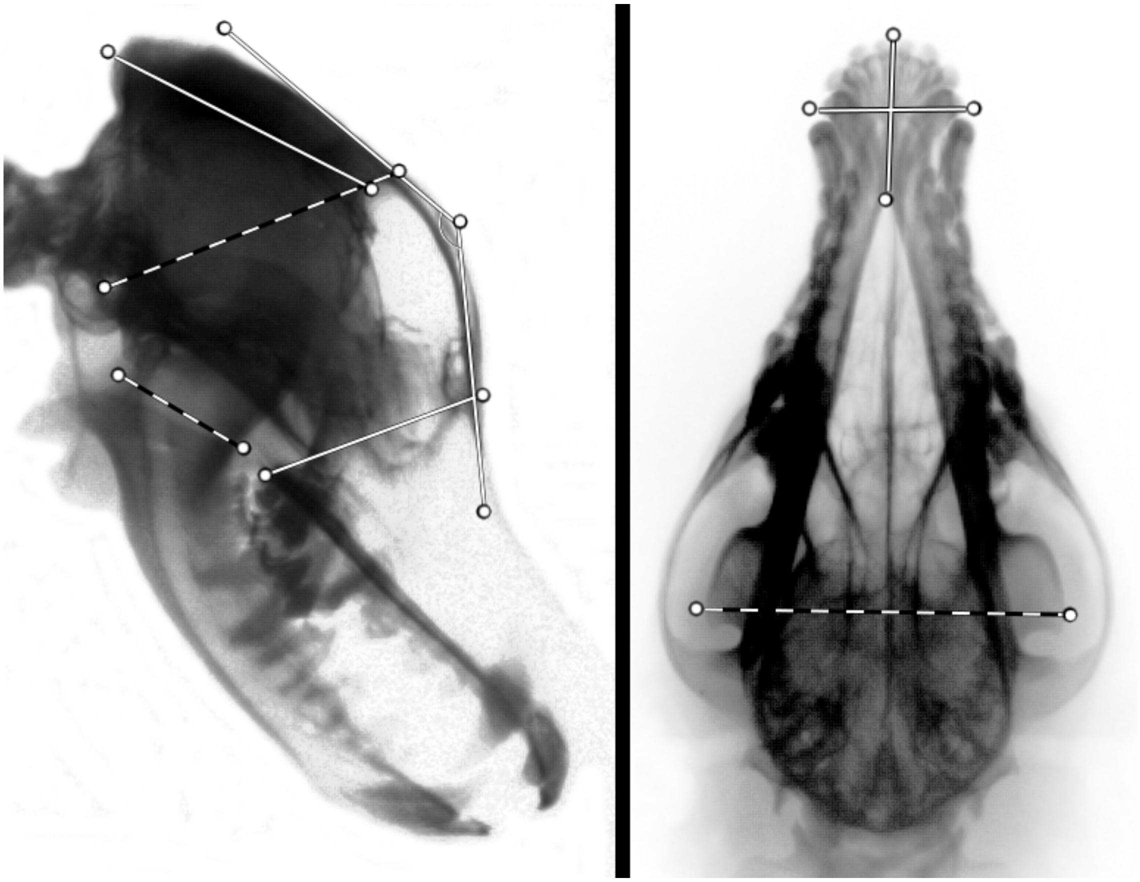

Figure 3.8. Lateral and dorsal radiograph images of female PWD skull highlighting skull and face variables varying significantly with laryngeal position. Solid lines and dotted lines indicate variables with opposing influences.

Chapter 4

Discussion

4.1 Overview

The goal of this thesis was to evaluate two independent theoretical explanations for the descent of the larynx found in humans. This was accomplished by analyzing the possible relationship between vocal tract length and body size (Chapter 2), as well as the possible relationship between laryngeal descent and cranio-facial form (Chapter 3), in two separate and unique radiographic Canid samples, the Portuguese Water Dog (PWD) and the Russian Silver Fox. PWDs were decimated in World War II and their recovery since that time has become the focus of study for the Georgie Project, a unique genetic and phenotypic cross-generational research program. Russian Silver Foxes were originally utilized by Dmitry Belyaev to investigate a possible route of domestication by tracking changes in the animal's aggression and fear towards humans. Through these two research programs, a large amount of information has been collected, including detailed radiographic images, making them especially suitable subjects for the current work.

4.1.1 Vocal Tract Length and Body Size

The first original research presented here describes the relationship between vocal tract length (VTL) and body size in PWDs and Silver Foxes. To move away from using weight as a definitive indicator of body size, femur and humerus length were combined via multiple regression analyses to represent body size. In both species, overall VTL was related to overall body size when species and sexes were analyzed separately. Whereas many previous studies have been limited to analyzing overall VTL, the current work involved subdividing the vocal tract into its constituent oral and pharyngeal cavities. The oral cavity was consistently related to body size in both species and both sexes, which is likely because the growth of the bony anatomy of the face is correlated with the growth of other bony structures, such as femur and humerus length. However, the pharyngeal cavity showed weaker and inconsistent relationships with body size. This outcome may reflect the fact that the pharyngeal cavity length is defined by the position of the larynx, which is determined by ligamentous connections of the hyoid skeleton to the skull base and mandible rather than by bone-bone connections. Hence, laryngeal position – and thus pharyngeal cavity size – may be emancipated to some extent from the bony constraints that control the size of the oral cavity.

These VTL and body size results support two aspects of Fitch's (1997) Body Size Exaggeration Hypothesis, namely that F_n may be related to body size but also be subject to manipulation in ways that exaggerate size via alterations of layrnx position and thus pharyngeal cavity length. Therefore, it is not only possible that the honesty of an animal's vocalization can be situation dependent via movement of the larynx, but it is also possible that animals may present both honest and dishonest information in a single vocalization.

Aspects of a vocalization that are derived from the oral component of the vocal tract can be seen as being relatively honest signals while aspects of a vocalization that are derived from the pharyngeal component of the vocal tract may be dishonest as they are more likely to be independent of body size. Similar effects have been observed in human speech, where the oral and pharyngeal cavities contribute differentially to vowel and phoneme quality (Fant, 1960). But this complicated relationship between vocal tract cavities and F_n has not been well explored in non-human animals.

4.1.2 Laryngeal Descent and Cranio-Facial Structure

The second original research presented here discusses an alternative to the traditional explanation for laryngeal descent in human ancestors, the Phonetic Expansion Hypothesis. Traditionally, incrementally increasing phonetic abilities have been considered the primary driver behind laryngeal descent. But some current research has shown that the initial descent of the larynx may not have increased the individual's phonetic abilities (Boe et al., 2007). The current research shows that the facial morphological alterations that occurred over the course of human evolution may have driven, at least initially, the descent of the larynx. In the current sample of PWDs, the descent of the larynx in male dogs was related to skull Principal Component 4 (PC4).

PC4 in males is characterized as a facial length-width trade-off where the face gets narrower as it is drawn forward and becomes longer; likewise, the face becomes wider as it shortens. The degree of laryngeal descent was positively associated with facial shortening and widening. These alterations in facial shape mirror what occurred over the course of human evolution since splitting with the great apes. Compared to our last common ancestor, modern human facial form has become flatter and wider. If a similar effect to that observed in the male PWDs operated on ancestral humans, the descent of the larynx can be explained, at least partially, by this facial flattening process.

4.2 Potential Shortcomings

4.2.1 Vocal Tract Length and Body Size

The current work improves on previous research in several ways but there remain potential shortcomings to address in the future. For example, the finding that vocal tract length correlates well with body size in radiographic images of anaesthetized canids may exaggerate the relationship that holds in awake and active in individuals. As confirmed here, the larynx is not in a fixed position and the angle of the head, which can change during vocalization in many species, can influence laryngeal position. Using a small sample of three dogs, Fitch (2000b) found that both head and larynx position change during vocalization. At the same time, additional analyses undertaken here show that this confound can be addressed in future work by using the residuals from a regression of larynx position on variable head flexion/extension, instead of the absolute measures of larynx position from radiogoraphic images.

However, it is also possible that animals may be able to voluntarily alter the position of their larynx without altering head position. People are able to do this when they speak by deliberately raising or lowering their larynx while voicing. Similar dynamic alterations to larynx position in vocalizing animals might upset the correlations between overall vocal tract length and body size established here from radiographic images of sedated individuals. Under normal circumstances, animals may also be able to manipulate other aspects of vocal anatomy (e.g., tongue and lips) to alter vocal tract length.

Notwithstanding these issues, the current work is the first of its kind to perform an in-depth analysis of the relationship between body size and not only overall VTL but also the length of its constituent oral and pharyngeal components in a large and well-balanced sample.

A further potential caveat concerns the traditional assumption that the resonance pattern of vocalizations is determined primarily by the length of the vocal tract through which the sounds propagate. Recently, it has come to light that this view may be too simple; there may be other influences on the F_n of voiced sounds beyond the linear length of the tube. For example, in Koalas, the measured F_n of some vocalizations point to a corresponding vocal tract length that exceeds the entire length of the animal's body, which is obviously physically impossible (Charlton et al., 2011). This outcome points to there being additional factors beyond simply vocal tract length that affect the F_n of the vocalizations produced.

One possibility is that resonance patterns might also depend, in part, on the cross sectional area (diameter) of the vocal tract tube. One might expect vocal tract length and width to covary linearly such that the issue becomes moot. But this might not always be the case. There may be instances where certain individuals have comparatively wide or comparatively narrow vocal tracts with corresponding differences in resonance patterns quite independently of any differences in vocal tract length.

A related concern is that vocal tracts often involve more complex configurations and side-branches than the traditional 'simple tube' model generally allows for. For example, in language, most phonemes involve articulations of the tongue, jaw, and lips in ways that distort the vocal tract from its neutral (unarticulated) configuration and thereby dramatically alter the F_n profiles of the sounds produced. Further, some phonemes, such as the nasalized consonants "m" and "n", involve coupling of the nasal cavities with the oral cavities, significantly altering effective vocal tract dimensions and thus the F_n patterns of the sounds produced (Lieberman, 1993). Although poorly studied, animal sounds may involve some similar articulations that alter the vocal tract configuration and thus its resonant properties (Fox & Cohen, 1977; Riede, Bronson, Hatzikirou, & Zuberbuhler, 2005; Sanvito et al., 2007). In short, the traditional model of the vocal tract as a simple tube open at one end is perhaps too simplistic.

4.2.2 Laryngeal Descent and Cranio-Facial Form

A potential shortcoming of the finding that larygeal position was affected by variable cranio-facial size and shape in PWD's is that the magnitude of the effect was relatively small (i.e., the degree of variation in laryngeal position was not dramatic). However, on theoretical grounds, the effect does not need to be very large in order for it to be significant in evolutionary terms, particularly if it is subject to continuing selection over many generations. In such circumstances, small incremental changes can accumulate and ultimately produce more dramatic modifications.

A second potential criticism of the laryngeal descent results is that the analysis assumes that changes in larynx position will be permanent and that, therefore, laryngeal descent can be seen in the resting position of the larynx. In humans, the majority of laryngeal descent seems to be permanent with a low resting position creating a large pharyngeal cavity and the larynx able to retract even deeper when required for speech. But, as evidenced by other animals, it is possible for the majority of laryngeal descent to be non-permanent.

In the classic example of European Red Deer, the larynx is permanently descended a short amount but the great majority of the descent occurs when the animal vocalizes and pulls its larynx down to the sternum (Fitch & Reby, 2001). It is possible that the weak effect of cranio-facial form on larynx position may be due to the levels of laryngeal descent in the sample not being fully identifiable because the animals rely on the temporary lowering of their larynx when they vocalize in contrast to the permanent descent of the larynx found in humans. An animal could potentially pay less of the associated costs of a descended larynx by relying on the temporary descent of the larynx.

4.3 Future Directions

There are ways to improve upon this research in the future that can counter the potential problems presented above. First, one natural extension of the current research would be to study the relationship between VTL and body size in active and vocalizing animals, there-by addressing the possibility of additional dynamic laryngeal descent that might further confirm or contradict the honest signaling relationships identified here. At the same time, this research should incorporate other dimensions of the vocal tract to better establish whether body-size related resonance patterns are well modeled by a vocal tract model based on a simple tube, or whether they are also influenced by other features, such as the width of the vocal tract or the coupling of the vocal tract with side branches such as the nasal cavity.

Arguably, the most exciting component of this work has been the identification of a relationship between facial shape and laryngeal position in dogs with provocative implications for the course of laryngeal descent in humans and its relevance to language evolution. At the moment, these results are limited to the domestic dog, but if alternative species show similar correlated laryngeal descent with the shortening of the facial structure, the current findings can be considered even more applicable to human evolution as an alternative to the Phonetic Expansion Hypothesis. Hence, an obvious extension of the work would involve testing a much wider variety of species similarly characterized by variable facial and skull morphologies to test the generality of the findings reported here for dogs. Repeated instances of laryngeal descent in response to modified cranio-facial form would certainly buttress the suggestion that the specific instance of laryngeal descent in humans is not unique nor then likely uniquely connected to the emergence of language.

One potential obstacle to this kind of work in other species is the availability of detailed measurements of a large number of cranio-facial dimensions. Such detailed measures were available for the PWD sample used here (Chase et al., 2002) and were likely critical to detecting the relatively small differences involved. Without such refined measures, the documented patterns of cranio-facial variation might be too coarse to reveal effects of the sort identified here.

Overall, the current research provides support for the hypothesized relationship between body size and vocal tract length. Further, it provided support for a hypothesized relationship between cranio-facial structure (specifically facial length/width) and laryngeal descent. In the process, the work has also shown the value of using radiographic images and canine samples, which are widely available, to address a variety of important questions in comparative and evolutionary anatomy. Such materials should be considered for future research on other topics.

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