



# On vocal production mechanisms of male rutting calls in two ruminant species



Roland Frey<sup>1</sup>, Ilya Volodin<sup>2</sup>, Elena Volodina<sup>3</sup>

<sup>1</sup> Leibniz Institute for Zoo and Wildlife Research (IZW), Berlin, Germany, frey@izw-berlin.de

<sup>2</sup> Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University

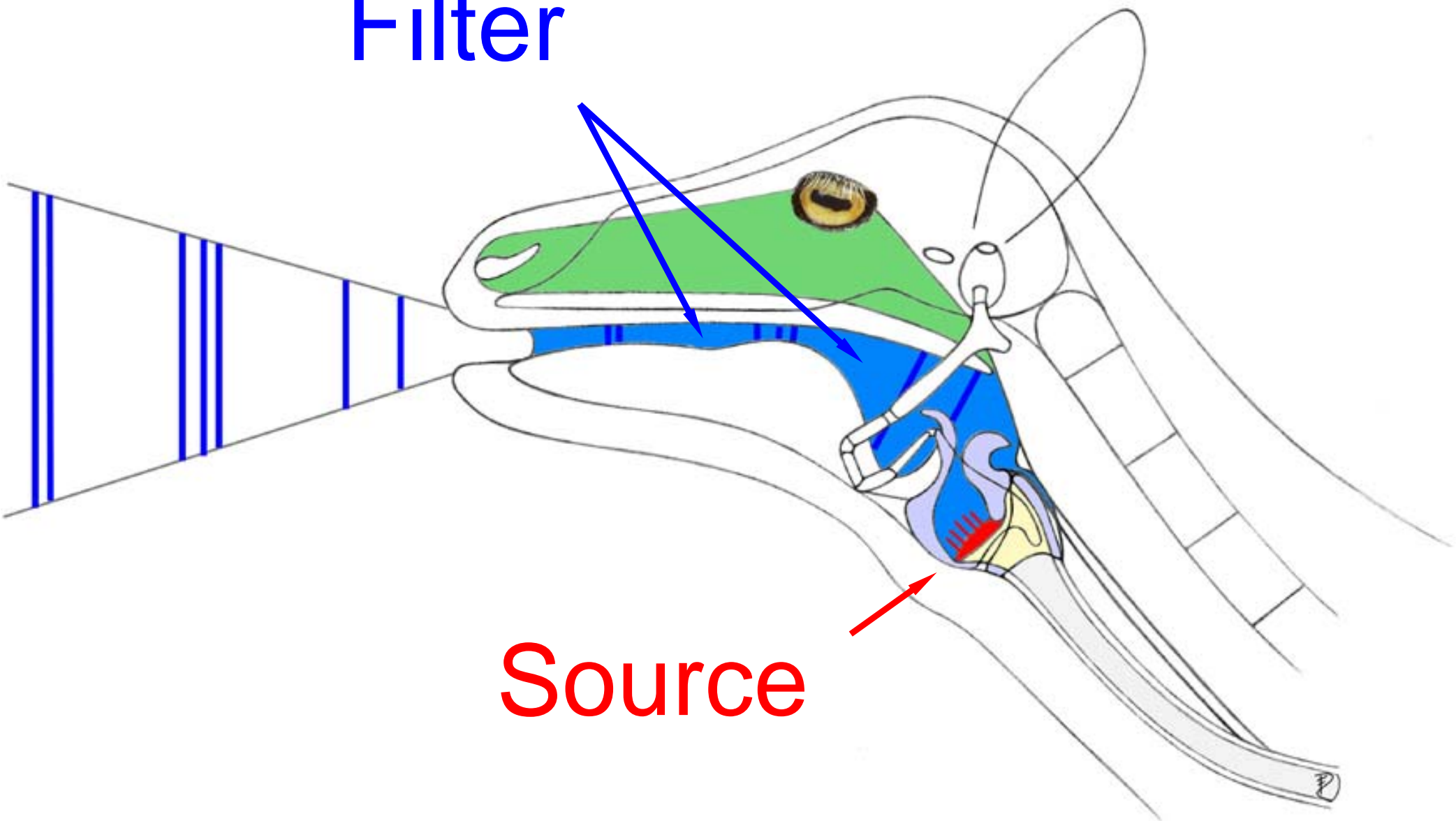
<sup>3</sup> Scientific Research Department, Moscow Zoo, Russia, volodinsvoc@gmail.com

# Introduction

- 1) Regarding emotional states in male mammals, rutting behaviour certainly ranks among the most intense as it directly correlates with reproductive success.
- 2) The males of some polygamous species, independently of each other, evolved specific morphological features of the vocal organs and associated mechanisms of vocal production.
- 3) These are of high relevance to male reproductive success and subjected to sexual selection both by male-male competition and female preference.

# Standard mammalian vocal production

Filter



Source

source-filter theory (J. Müller, 1848; Fant 1960)



# Independent evolution of larynx retraction

Convergent, the males of two polygamous species from two different families of ruminants evolved a mobile larynx and corresponding vocal tract transformations.

red deer (*Cervus elaphus*)

goitred gazelle (*Gazella subgutturosa*)



These results reveal: larynx descent is not necessarily associated with speech evolution.

# Vocal anatomy of male red deer I

1) low larynx resting position

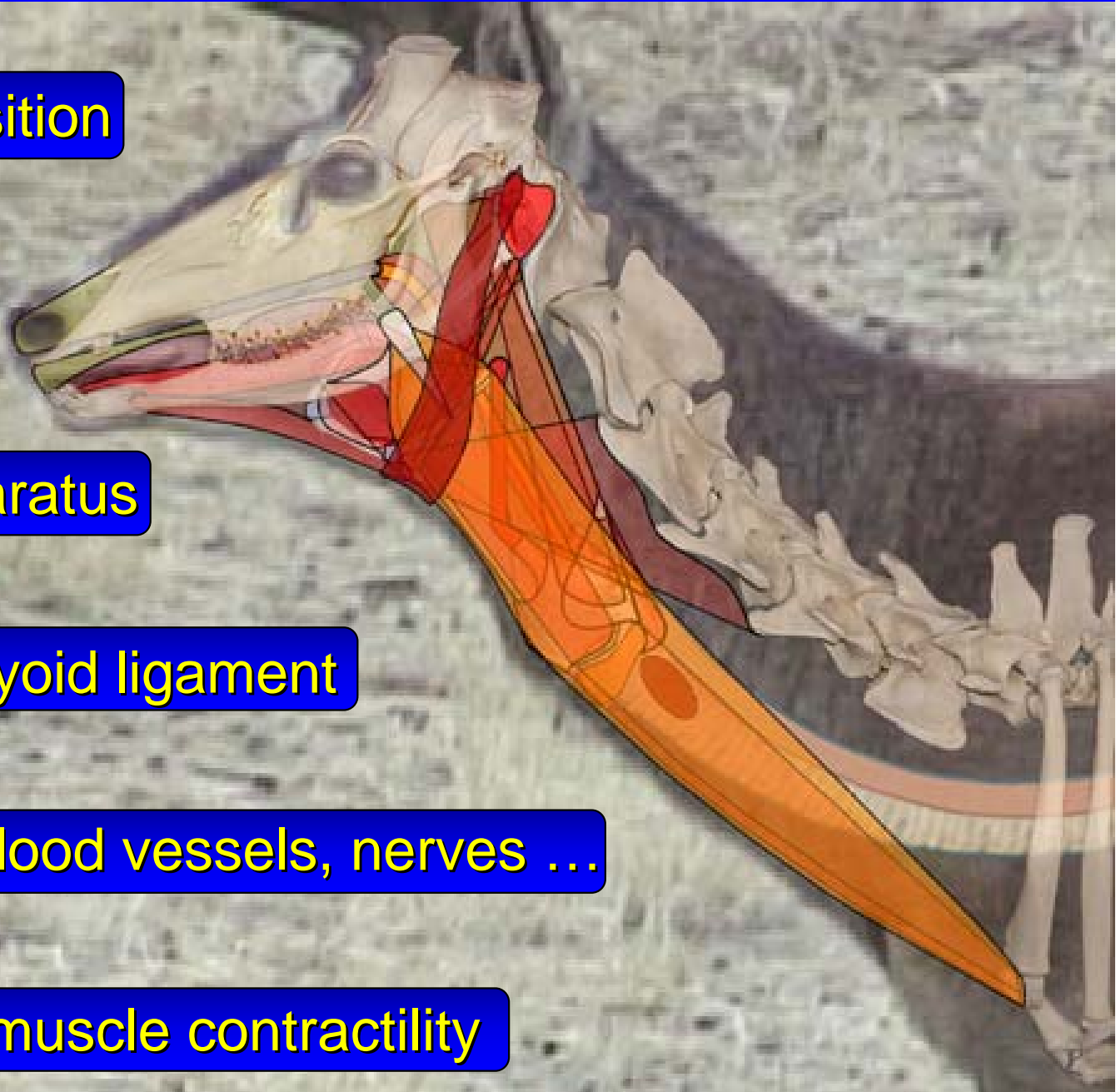
2) elongated soft palate

3) extensible hyoid apparatus

4) highly resilient thyrohyoid ligament

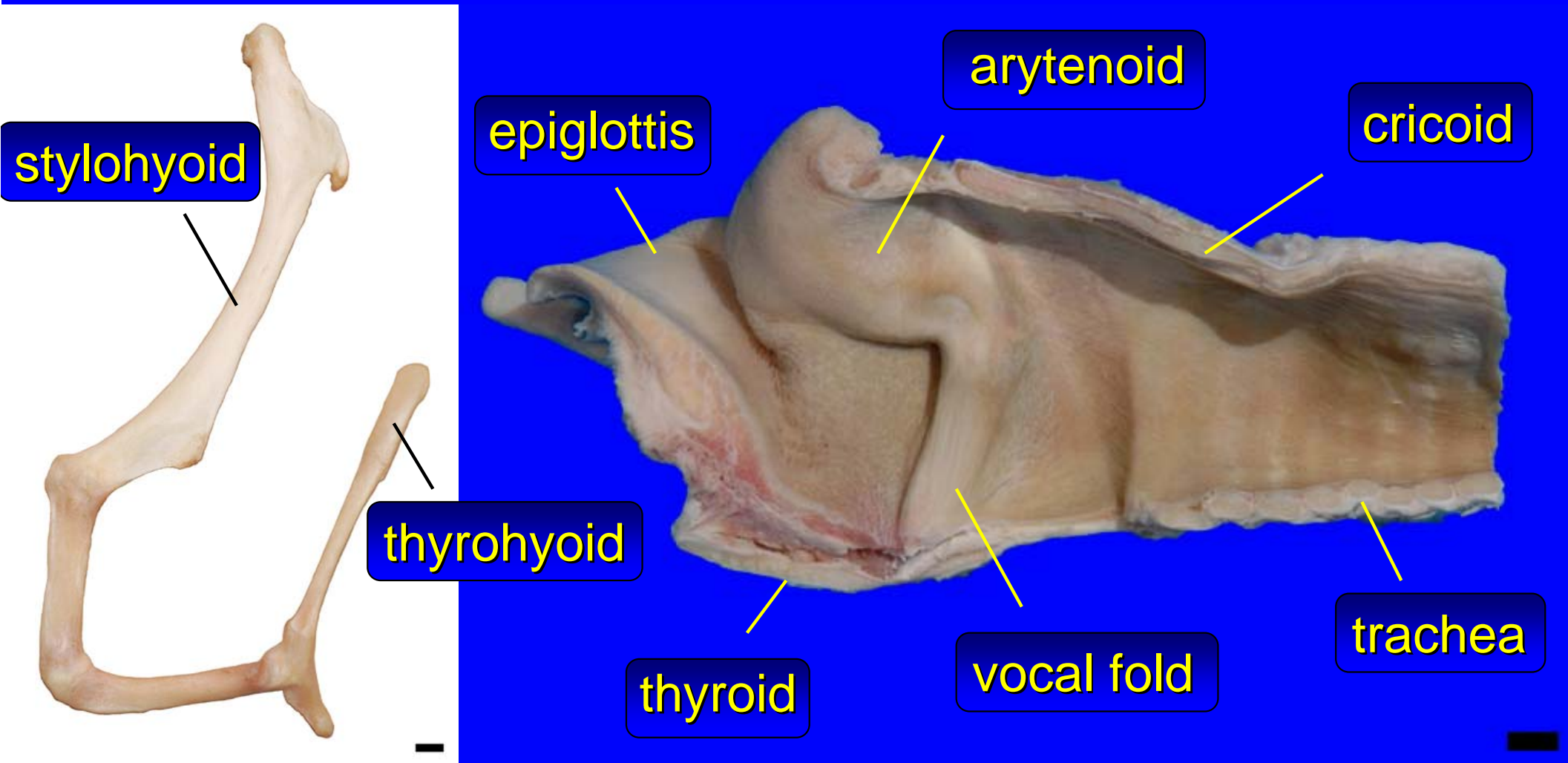
5) extensible pharynx, blood vessels, nerves ...

6) extremely high strap muscle contractility



Frey R, Volodin I, Volodina E, Carranza J, Torres-Porras J (2012) Vocal anatomy, tongue protrusion behaviour and the acoustics of rutting roars in free-ranging Iberian red deer stags (*Cervus elaphus hispanicus*). J Anat 220, 271-292.

# Vocal anatomy of male red deer II



Hyoid apparatus,  
left half, lateral view

Larynx,  
right half, medial view





# Vocal production in male red deer



1) neck extension

2) strap muscle contraction

3) extension of hyoid apparatus

4) expansion of pharynx

5) extension of pharynx

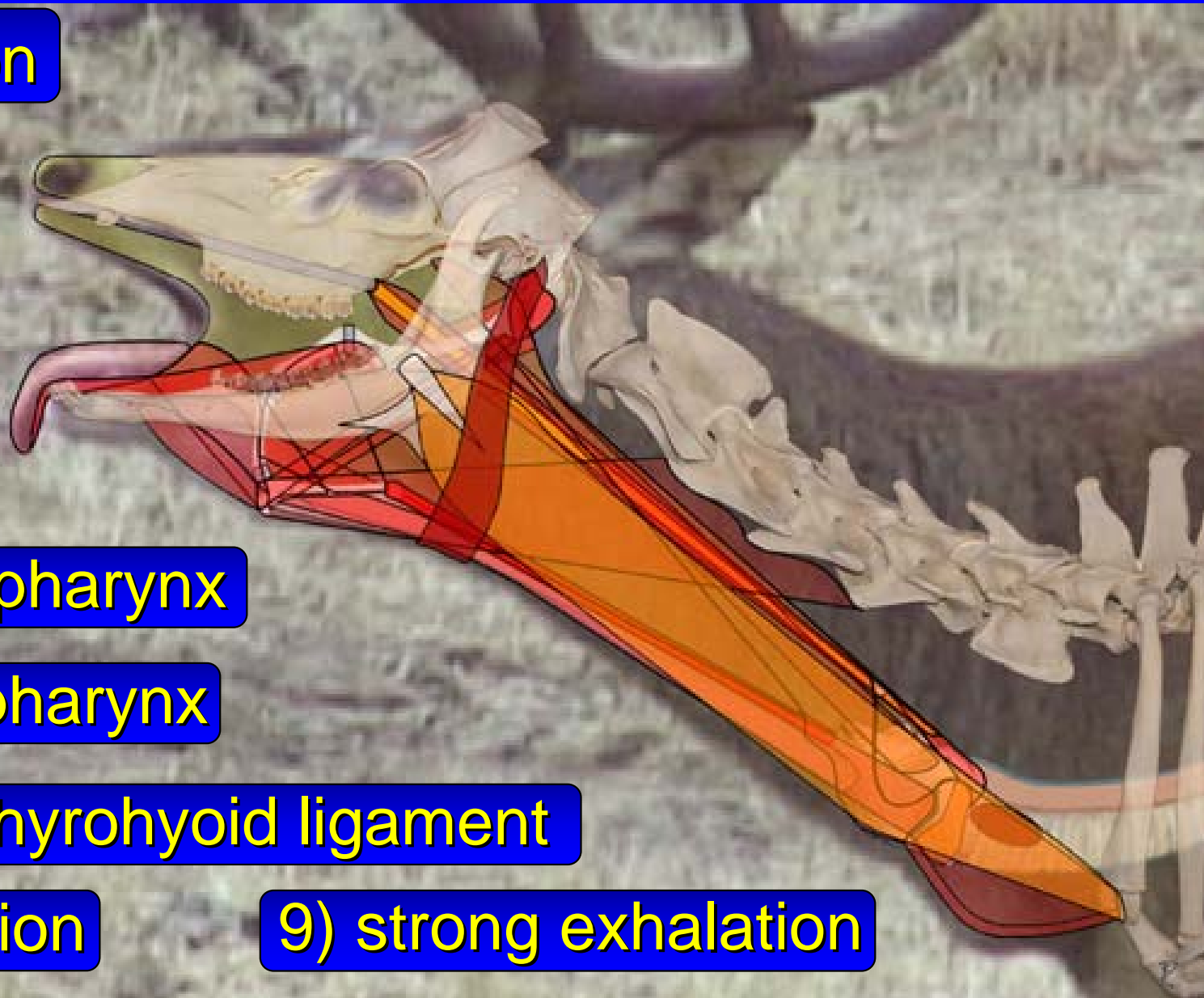
6) extension of thyrohyoid ligament

7) larynx retraction

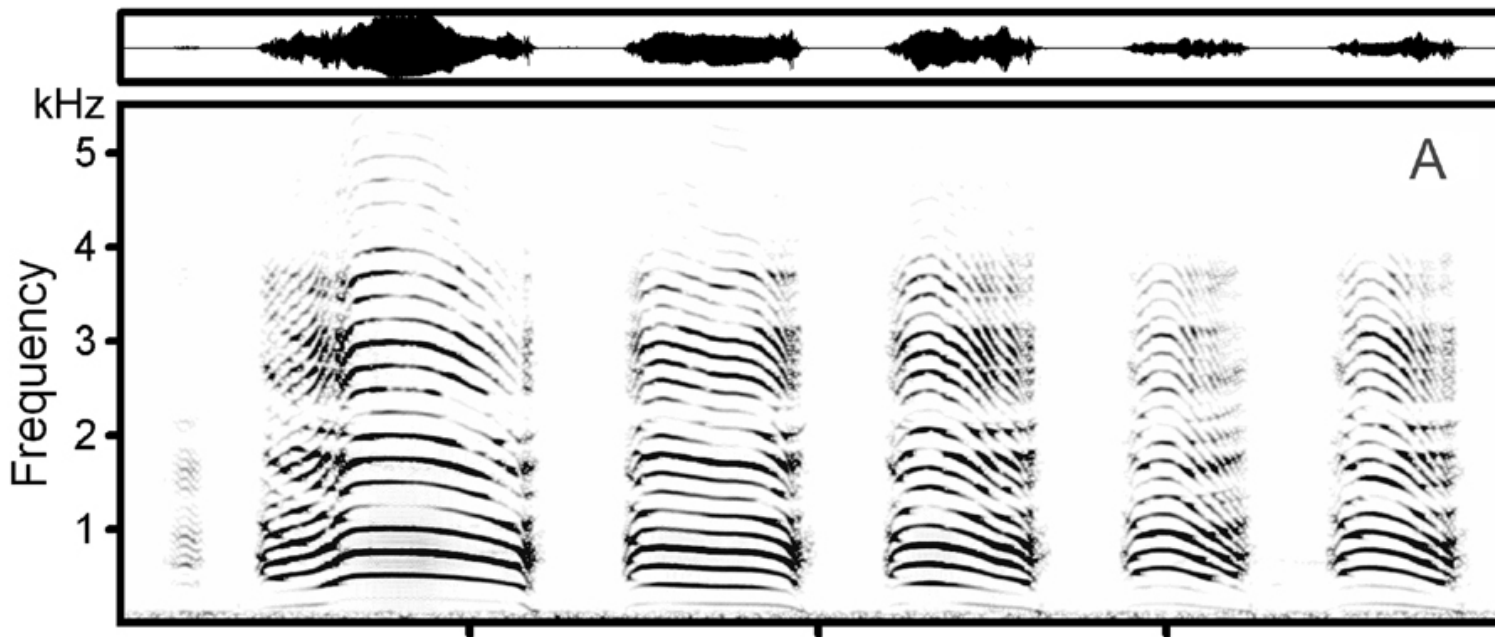
9) strong exhalation

8) soft palate elongation

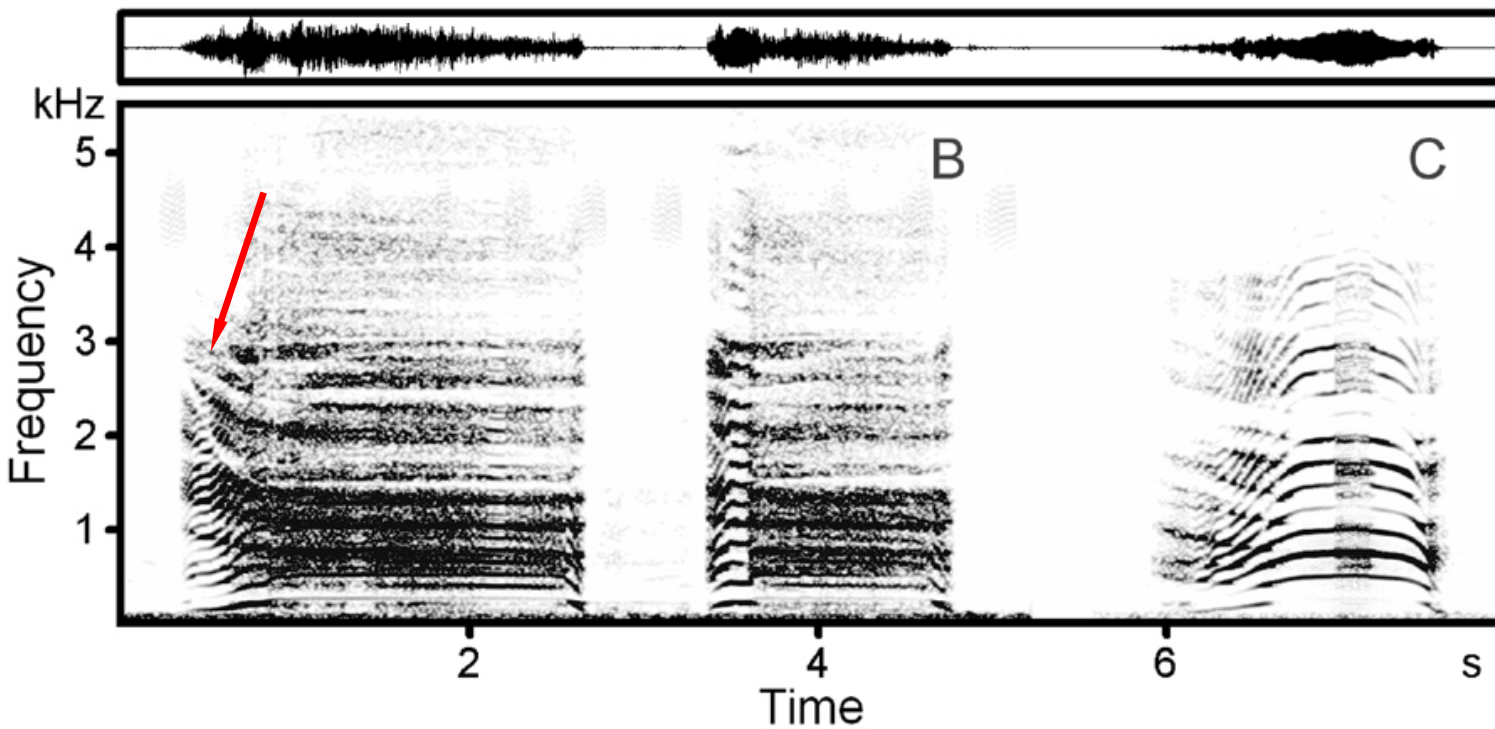
10) intrinsic muscle contraction



# Sonagram of adult male red deer



A common roars



B harsh roars







# Vocal anatomy of male goitred gazelle I

1) low larynx resting position

2) elongated soft palate

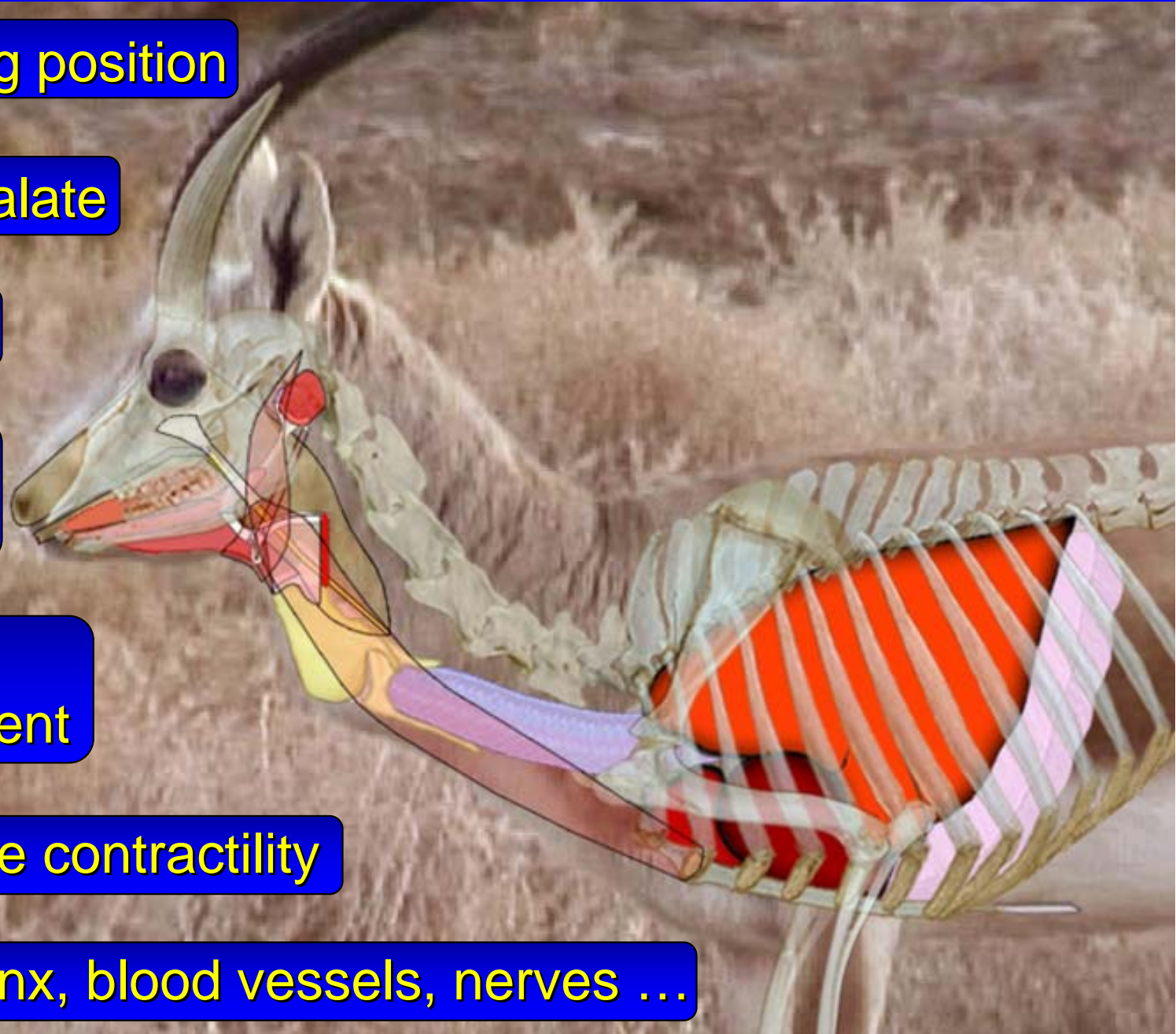
3) enlarged larynx

4) extensible hyoid apparatus

5) highly resilient thyrohyoid ligament

6) high strap muscle contractility

7) extensible pharynx, blood vessels, nerves ...

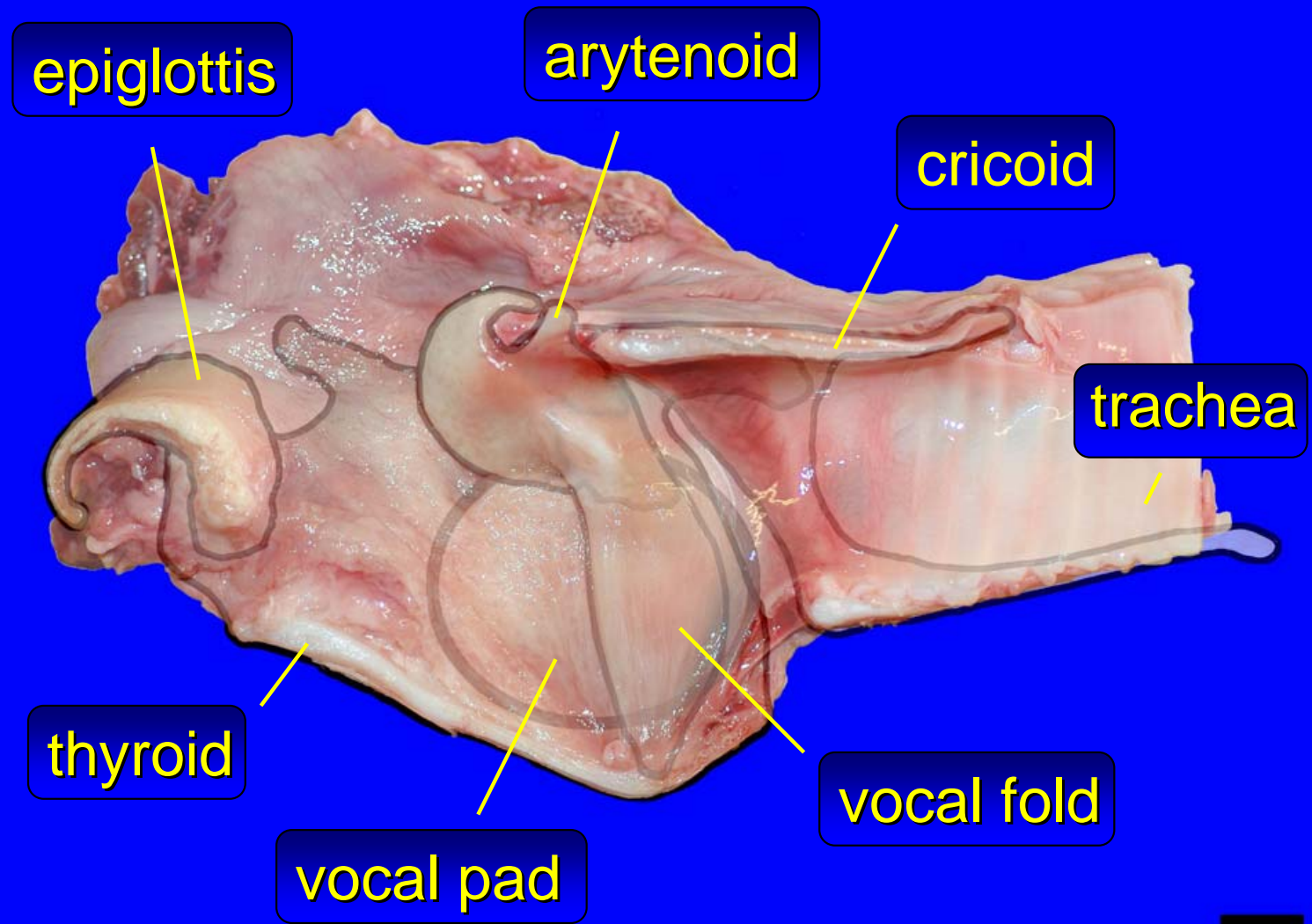




# Vocal anatomy of male goitred gazelle II



Hyoid apparatus,  
left half, lateral view



Larynx,  
right half, medial view

# Vocal production in male goitred gazelle

1) neck extension

9) intrinsic muscle contraction

2) strap muscle contraction

10) strong exhalation

3) hyoid  
extension

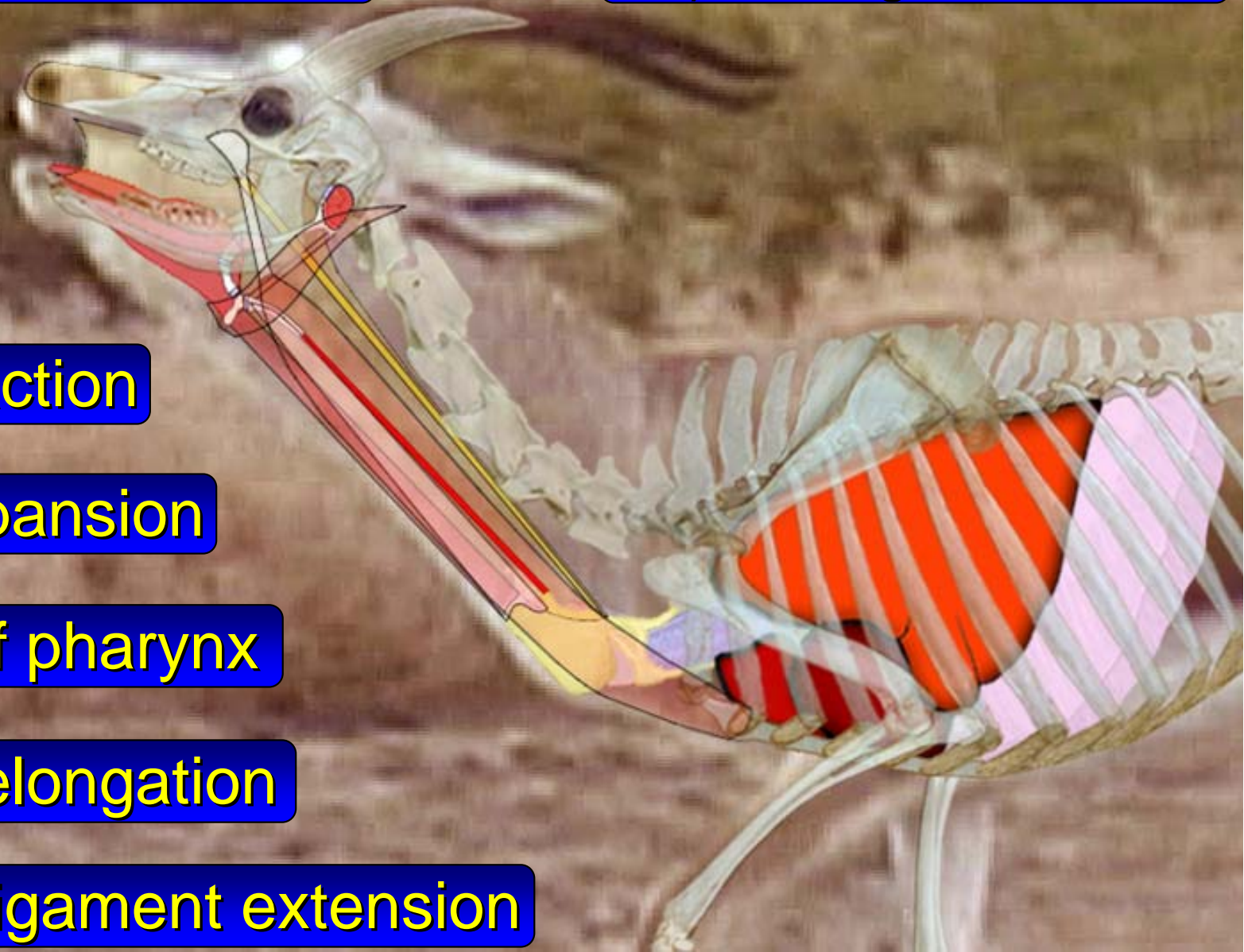
4) larynx retraction

5) pharynx expansion

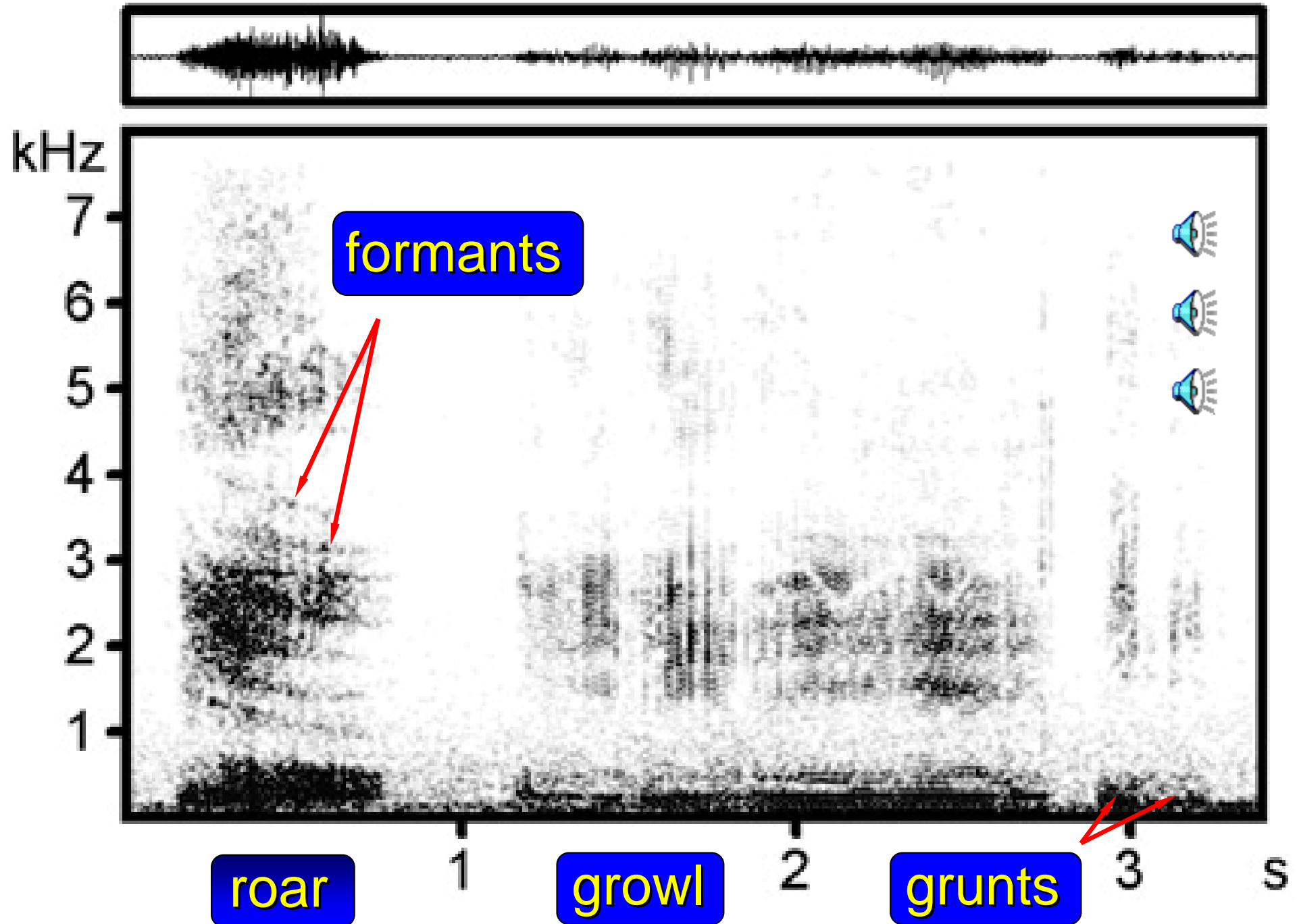
6) extension of pharynx

7) soft palate elongation

8) thyrohyoid ligament extension



# Sonagram of adult male goitred gazelle





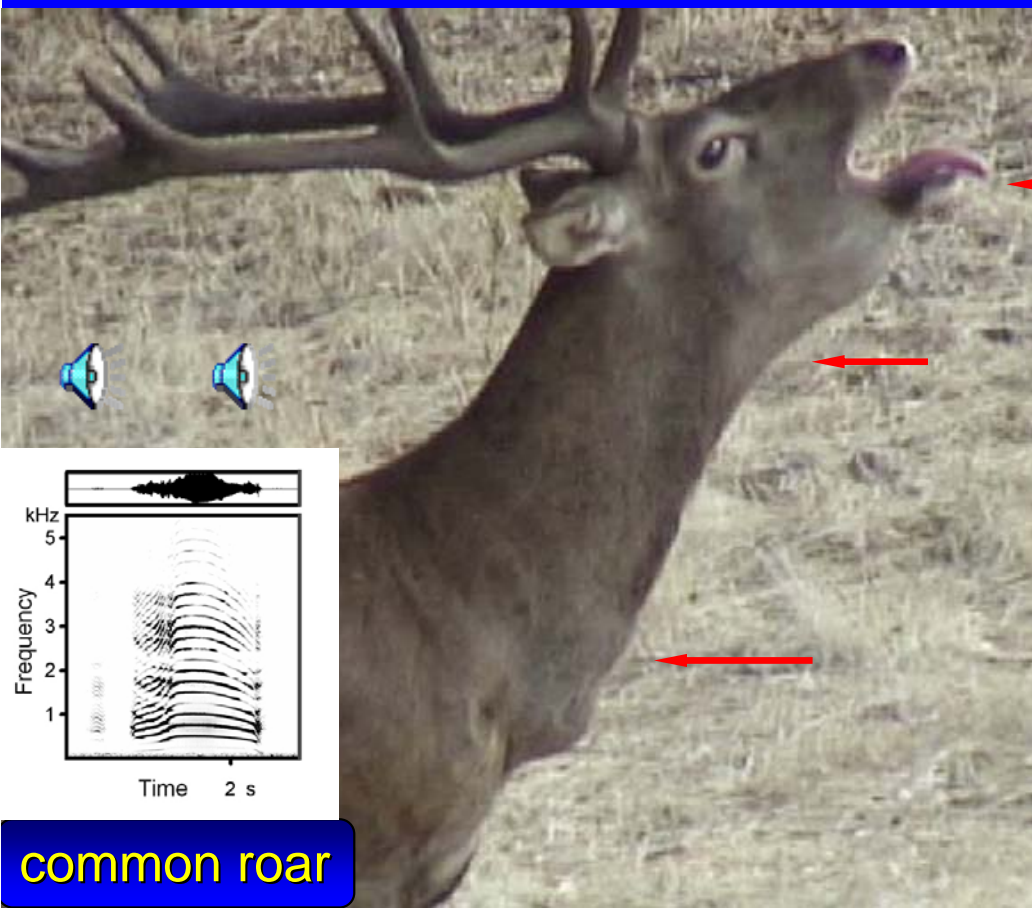




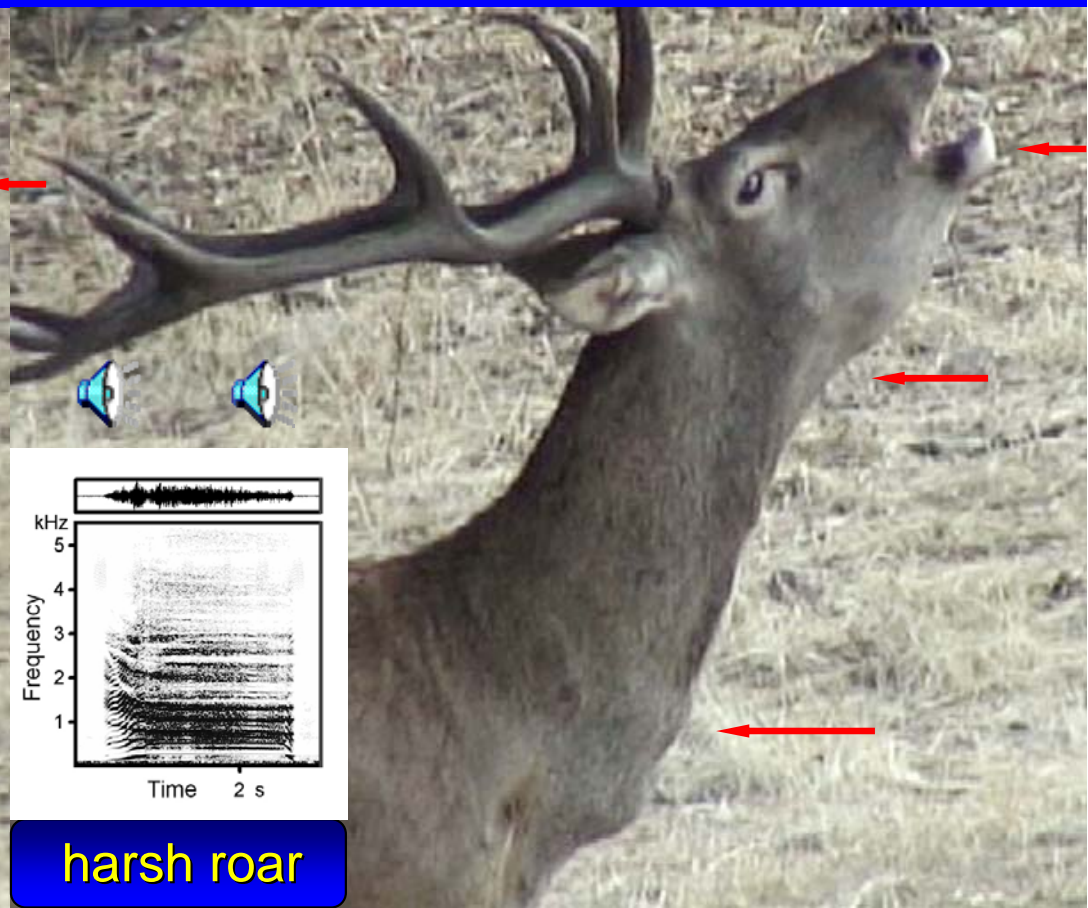
# Common and harsh roars in red deer

In the presence of rival males red deer stags produce special harsh roars destined to sound particularly intimidating.

Accordingly, a state of higher arousal evokes a specific call type that is audibly different from a more relaxed call.



common roar



harsh roar



# Acknowledgements

Staff of Ecocenter 'Djeiran',  
Bukhara, Uzbekistan,  
particularly

Natalia V. Soldatova  
Erkin T. Juldashev

Andrey Bushuev,  
Kseniya O. Efremova, Moscow

Doñana Biological Station (EBD),  
Staff at Doñana Biological Reserve,  
Spanish and Portuguese helpers:  
Marta V. Barroso, Anna M. Barbosa,  
Mónica E. Granados, Francisco JJ  
Moreno, Javier P. Gonzalez

Owners, managers and guards of several  
estates where materials have been collected

Juan Carranza,  
Jerónimo Torres-Porras  
Córdoba University, Spain

Consejería de Medio  
Ambiente, Junta de  
Andalucía, Spain

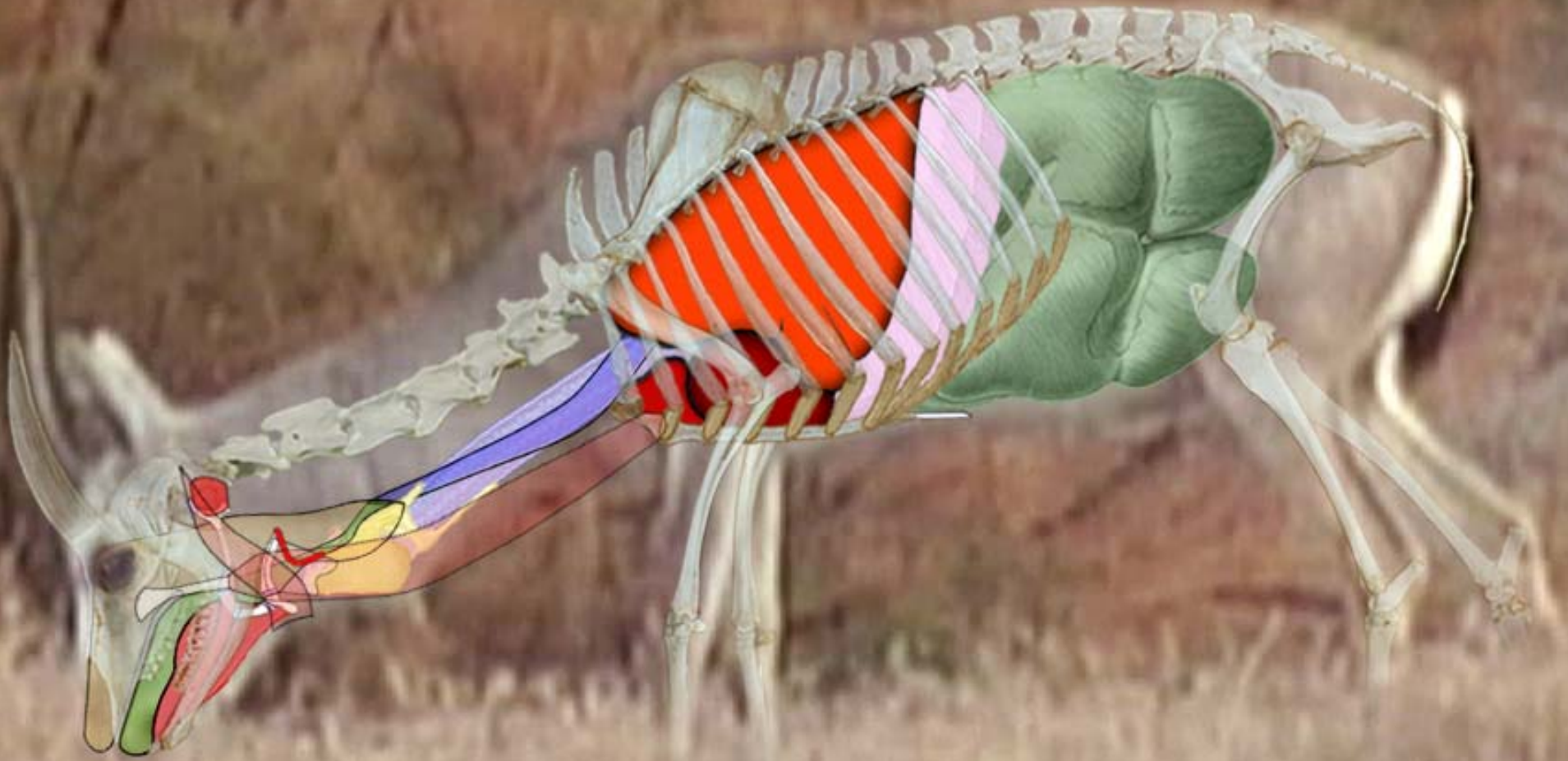
B. Blaszkiewicz,  
Director of Tier-  
park Berlin,  
Germany

CT-Center, IZW  
G. Galateanu  
G. Fritsch,





# Feeding position of larynx in goitred gazelle



Owing to gravity, hyoid apparatus, hyoid ligament, pharynx and larynx sag and are shifted towards the head

# Male-male competition



Video fighting Iberian red deer stags



# Male-male competition



Video fighting goitred gazelle males

# Female preference



Response of estrous female red deer (*Cervus elaphus*) to male roars in which an acoustic cue to body size, the formants, had been re-scaled to simulate different size callers, reveals that hinds prefer roars simulating larger callers.



This is the first evidence use an acoustic cue to choice context.



that female mammals body size in a mate

Sexual selection through female mating preferences may have provided an additional selection pressure along with male-male competition for broadcasting size-related information in red deer and other mammals.

# Intersexually differing behavioural strategies

In mammals there is an initial asymmetry in reproductive investment. As a result, the reproductive success of females will usually be limited by the number of young they can produce and raise, that of males will often be limited by factors affecting the number of females they can fertilise. This also explains why, among mammals, polygyny is common and polyandry rare.



intra-sexual competition  
variance in reprod. success  
energy expenditure during rut  
fighting ability  
early growth rate  
winter mortality



# Differing reproductive strategies of males and females in red deer (*Cervus elaphus*)

The theory of natural selection provides an explanation for differences between species, but not for variation between the sexes.

In most species, males and females live in the same habitat and are subject to similar environmental pressures – why should there be any sexual dimorphism?

The costs of reproduction to members of each sex are different.

Parental investment of males is low (fertilization, copulation).

Parental investment of females is high (gestation, lactation).

A male's reproductive success is usually limited by the number of breeding females to which he can gain access.

Direct competition

A female's reproductive success is more related to her ability to rear offspring and depends on the efficiency of food collection and processing.

Indirect competition



monogamous or territorial

# Polygyny

(few males fertilize multiple females and many males fertilizing few or none)

Frequently, a polygynous mating system is associated with intense male-male competition and female choice.

As a consequence of the choices that females make and of the efforts that males put into acquiring female mating partners, many mammalian species have complex behaviours and morphologies related to reproduction.

Many mammalian species are marked by sexual dimorphism as a result of selection for males that can better compete for access to females.



polygynous

# Sexual selection

The advantage which certain individuals have over others of the same sex and species, in exclusive relation to reproduction (Darwin, 1871).

A form of natural selection that occurs when individuals vary in their ability to compete with others for mates or in their attractiveness to members of the opposite sex.

As with natural selection, sexual selection leads to genetic changes in the population over time.

Intrasexual selection, competition for copulation, dominance (e.g.: red deer, Mongolian gazelle)

Intersexual selection, competition by mate choice, female choice (e.g.: red deer)