Refdeervocal

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KEYWORDS: Reby, red deer

Record 1 of 12

Reby, D; Charlton, BD; Locatelli, Y; McComb, K. 2010. Oestrous red deer hinds prefer male roars with higher fundamental frequencies. *PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES* 277 (1695): 2747-2753..

Author Full Name(s): Reby, David; Charlton, Benjamin D.; Locatelli, Yann; McComb, Karen

Author Keywords: red deer; vocal communication; fundamental frequency; female mating preferences

KeyWords Plus: VOCAL-TRACT LENGTH; CERVUS-ELAPHUS; VOICE PITCH; FEMALE CHOICE; BODY-SIZE; LUTEINIZING-HORMONE; HUNTER-GATHERERS; MENS VOICES; ESTRUS; SYNCHRONIZATION

Abstract: Across vertebrates, the observation that lower-pitched vocalizations are typically associated with larger and/or higher quality males has lead to the widespread belief that inter-and intra-sexual selection will produce male calls with low fundamental frequencies (F0). Here we investigated the response of oestrous red deer hinds to playback of re-synthesized male roars characterized by either higher than average or lower than average F0. We found that hinds prefer higher rather than lower 'pitched' roars, providing, to our knowledge, the first evidence of such a bias in nonhuman mammals. Our findings can be interpreted in relation to previous observations that the minimum F0 of roars is positively correlated with male reproductive success in free-ranging red deer stags, and that across Cervids the F0 of male mating calls shows extreme variability. Females showing preferences for higher-pitched roars might derive genetic benefits through more competitive male offspring. Our results emphasize the need for further investigations of female preferences in mammals in order to better understand the extreme variation of F0 values observed in male sexual calls.

Times Cited: 0

Record 2 of 12

Vannoni, E; McElligott, AG. 2008. Low Frequency Groans Indicate Larger and More Dominant Fallow Deer (Dama dama) Males. *PLOS ONE* 3 (9): art. no.-e3113..

Author Full Name(s): Vannoni, Elisabetta; McElligott, Alan G.

KeyWords Plus: VOCAL-TRACT LENGTH; BABOON LOUD CALLS; BODY-SIZE; RED DEER; MATING SUCCESS; VOICE PITCH; ACOUSTIC FEATURES; SEXUAL SELECTION; DESCENDED LARYNX; RHESUS MACAQUES

Abstract: Background: Models of honest advertisement predict that sexually selected calls should signal male quality. In most vertebrates, high quality males have larger body sizes that determine higher social status and in turn higher reproductive success. Previous research has emphasised the importance of vocal tract resonances or formant frequencies of calls as cues to body size in mammals. However, the role of the acoustic features of vocalisations as cues to other quality-related phenotypic characteristics of callers has rarely been investigated.

Methodology/Principal Findings: We examined whether the acoustic structure of fallow deer groans provides reliable information on the quality of the caller, by exploring the relationships between male quality (body size, dominance rank, and mating success) and the frequency components of calls (fundamental frequency, formant frequencies, and formant dispersion). We found that body size was not related to the fundamental frequency of groans, whereas larger males produced groans with lower formant frequencies and lower formant dispersion. Groans of high-ranking males were characterised by lower minimum fundamental frequencies and to a lesser extent, by lower formant dispersions. Dominance rank was the factor most strongly related to mating success, with higher-ranking males having higher mating success. The minimum fundamental frequency and the minimum formant dispersion were indirectly related to male mating success (through dominance rank).
Conclusion/Significance: Our study is the first to show that sexually selected vocalisations can signal social dominance in mammals other than primates, and reveals that independent acoustic components encode accurate information on different phenotypic aspects of male quality.

Times Cited: 10

Record 3 of 12

Kidjo, N; Cargnelutti, B; Charlton, BD; Wilson, C; Reby, D. 2008. VOCAL BEHAVIOUR IN THE ENDANGERED CORSICAN DEER: DESCRIPTION AND PHYLOGENETIC IMPLICATIONS. *BIOACOUSTICS-THE INTERNATIONAL JOURNAL OF ANIMAL SOUND AND ITS RECORDING* 18 (2): 159-181..

Author Full Name(s): Kidjo, Nicolas; Cargnelutti, Bruno; Charlton, Benjamin D.; Wilson, Christian; Reby, David

Author Keywords: Corsican Deer; Red Deer; vocal repertoire; Cervus elaphus corsicanus; formant frequency; vocal tract

KeyWords Plus: CERVUS-ELAPHUS-CORSICANUS; RED DEER; BODY-SIZE; MAMMALS; PHYLOGEOGRAPHY; COMMUNICATION; VOCALIZATIONS; EVOLUTION; GROANS; STAGS

Abstract: Here we present the first description of the vocal behaviour of the Tyrrhenian subspecies of Red Deer, the Corsican Deer. Vocalisations from calves, hinds and stags were recorded. Their acoustic characteristics were analysed in order to contrast these with published data characterising central European Red Deer hind and calve contact calls and Scottish Red Deer stag mating calls. We found that the vocal repertoire of Corsican Deer was very comparable with that of central European and Scottish Red Deer, with the exception of one call type, the harsh roar, absent in the Corsican Deer repertoire. Because Corsican Deer are the smallest subspecies of Red Deer, we expected calls to be characterised by higher spectral components. However, while male roars did have higher vocal tract resonances, consistent with a shorter vocal tract, we found that the fundamental frequency (F0) was much lower than predicted, in fact the lowest recorded in any studied Red Deer subspecies. We also found a strong sexual dimorphism in F0, with male calls approximately twice as low as female calls, suggesting that the low F0 observed in Corsican male roars is a result of sexual selection for lower-pitched males. The results of this study emphasise the phenotypic originality of Corsican Deer, and strengthen the case for its conservation. We also argue that future studies should compare the vocal behaviour of Corsican Deer with that of other circum-Mediterranean populations.

Times Cited: 3

Record 4 of 12

Charlton, BD; McComb, K; Reby, D. 2008. Free-ranging red deer hinds show greater attentiveness to roars with formant frequencies typical of young males. *ETHOLOGY* 114 (10): 1023-1031..

Author Full Name(s): Charlton, Benjamin D.; McComb, Karen; Reby, David

KeyWords Plus: MONKEYS CERCOPITHECUS-AETHIOPS; HUMANS HOMO-SAPIENS; VOCAL-TRACT LENGTH; MATE CHOICE; ACOUSTIC CLASSIFICATION; RHESUS MACAQUES; ALARM CALLS; DISCRIMINATION; VOWEL; HONEST

Abstract: Acoustic cues present in the reproductive calls of many animal species potentially encode important information about the caller. Here, we test the response of a free-ranging population of peri-oestrus red deer hinds to variation in a specific acoustic cue to body size in the male roar, the formant frequencies. Our results revealed: (1) that hinds showed greater overall attention (judged by longer looking responses and lower response latencies) to roars simulating males of sub-adult body size than to those simulating a large adult male and (2) that hinds without dependent offspring had greater looking responses to male roars and lower response latencies than hinds with dependent offspring to roars simulating sub-adult males. These findings indicate that free-ranging red deer hinds may use formants as acoustic cues to gauge the body size and maturity of males in their natural environment, possibly to facilitate earlier detection and avoidance of young stags that are known to harass them.

Times Cited: 5

Record 5 of 12

Charlton, BD; Reby, D; McComb, K. 2008. Effect of combined source (F0) and filter (formant) variation on red deer hind responses to male roars. *JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA* 123 (5): 2936-2943, Part 1..

Author Full Name(s): Charlton, Benjamin D.; Reby, David; McComb, Karen

KeyWords Plus: VOCAL-TRACT LENGTH; BODY-SIZE; SEXUAL SELECTION; MATE CHOICE; ACOUSTIC ALLOMETRY; DESCENDED LARYNX; CERVUS-ELAPHUS; DAMA-DAMA; EVOLUTION; FREQUENCY

Abstract: Studying female response to variation in single acoustic components has provided important insights into how sexual selection operates on male acoustic signals. However, since vocal signals are typically composed of independent components, it is important to account for possible interactions between the studied parameter and other relevant acoustic features of vocal signals. Here, two key components of the male red deer roar, the fundamental frequency and the formant frequencies (an acoustic cue to body size), are independently manipulated in order to examine female response to calls characterized by different combinations of these acoustic components. The results revealed that red deer hinds showed greater overall attention and had lower response latencies to playbacks of roars where lower formants simulated larger males. Furthermore, female response to male roars simulating different size callers was unaffected by the fundamental frequency of the male roar when it was varied within the natural range. Finally, the fundamental frequency of the male roar had no significant separate effect on any of the

female behavioral response categories. Taken together these findings indicate that directional intersexual selection pressures have contributed to the evolution of the highly mobile and descended larynx of red deer stags and suggest that the fundamental frequency of the male roar does not affect female perception of size-related formant information. (c) 2008 Acoustical Society of America.

Times Cited: 7

Record 6 of 12

Charlton, BD; Reby, D; McComb, K. 2007. Female perception of size-related formant shifts in red deer, Cervus elaphus. *ANIMAL BEHAVIOUR* 74: 707-714, Part 4..

Author Full Name(s): Charlton, Benjamin D.; Reby, David; McComb, Karen

Author Keywords: acoustic cues; body size; Cervus elaphus; formant frequency; perception; red deer; vocal communication

KeyWords Plus: VOCAL-TRACT LENGTH; ACOUSTIC STRUCTURE; RHESUS MACAQUES; MONKEYS CERCOPITHECUS; PLAYBACK EXPERIMENTS; GRUNT VOCALIZATIONS; SPEECH-PERCEPTION; MACACA-MULATTA; VERVET MONKEYS; DISCRIMINATION

Abstract: Little is known about the role of specific acoustic cues in mammal vocal communication systems. In the current study, we used resynthesized male red deer roars in a habituation-discrimination paradigm to determine whether female red deer are sensitive to shifts in formant frequencies corresponding to the natural variation between the vocal tract lengths of a small and large adult red deer male. Hinds habituated to a given size variant showed a significant dishabituation when they were presented with roars in which the formants had been modified to simulate the other size variant. The signficant reduction in behavioural response to final rehabituation playback showed this was not a chance rebound in response levels. Our results suggest that formants are salient for red deer hinds and that hinds can detect a shift in formant frequencies that may have biological significance. We discuss the possible functions of formant perception in female red deer and more generally in nonhuman mammals.

Times Cited: 12

Record 7 of 12

Charlton, BD; Reby, D; McComb, K. 2007. Female red deer prefer the roars of larger males. *BIOLOGY LETTERS* 3 (4): 382-385..

Author Full Name(s): Charlton, Benjamin D.; Reby, David; McComb, Karen

Author Keywords: red deer; female mating preferences; vocal communication; formant frequencies; acoustic cues to body size

KeyWords Plus: VOCAL-TRACT LENGTH; ACOUSTIC STRUCTURE; CERVUS-ELAPHUS; MATE CHOICE; VOCALIZATION; STAGS; INFORMATION; CUES

Abstract: Surprisingly little is known about the role of acoustic cues in mammal female mate choice. Here, we examine the response of female red deer (Cervus elaphus) to male roars in which an acoustic cue to body size, the formants, has been re-scaled to simulate different size callers. Our results show that oestrous red deer hinds prefer roars simulating larger callers and

constitute the first evidence that female mammals use an acoustic cue to body size in a mate choice context. We go on to suggest that 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.

Times Cited: 25

Record 8 of 12

Vannoni, E; McElligott, AG. 2007. Individual acoustic variation in fallow deer (Dama dama) common and harsh groans: A source-filter theory perspective. *ETHOLOGY* 113 (3): 223-234..

Author Full Name(s): Vannoni, Elisabetta; McElligott, Alan G.

KeyWords Plus: VOICE PERTURBATION MEASUREMENTS; VOCAL-TRACT LENGTH; BABOON LOUD CALLS; RED DEER; DISCRIMINANT-ANALYSIS; DESCENDED LARYNX; MATING SUCCESS; CERVUS-ELAPHUS; ALARM CALLS; ROE DEER

Abstract: Mammals are able to distinguish conspecifics based on vocal cues, and the acoustic structure of mammal vocalizations is directly affected by the anatomy and action of the vocal apparatus. However, most studies investigating individual patterns in acoustic signals do not consider a vocal production-based perspective. In this study, we used the source-filter model of vocal production as a basis for investigating the acoustic variability of fallow deer groans. Using this approach, we quantified the potential of each acoustic component to carry information about individual identity. We also investigated if cues to individual identity carry over among the two groan types we describe: common and harsh groans. Using discriminant function analysis, we found that variables related to the fundamental frequency contour and the minimum frequencies of the highest formants contributed most to the identification of a given common groan. Common groans were individually distinctive with 36.6% (53.6% with stepwise procedure) of groans assigned to the correct individual. This level of discrimination is approximately six times higher than that predicted by chance. In addition, univariate ANOVAS showed significant inter-individual variation in the minimum formant frequencies when common and harsh groans were combined, suggesting that some information about individuality is shared between groan types. Our results suggest that the sound source and the vocal tract resonances act together to determine groan individuality and that enough variation exists to potentially allow individual recognition based on groans.

Times Cited: 15

Record 9 of 12

Reby, D; Andre-Obrecht, R; Galinier, A; Farinas, J; Cargnelutti, B. 2006. Cepstral coefficients and hidden Markov models reveal idiosyncratic voice characteristics in red deer (Cervus elaphus) stags. *JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA* 120 (6): 4080-4089..

Author Full Name(s): Reby, David; Andre-Obrecht, Regine; Galinier, Arnaud; Farinas, Jerome; Cargnelutti, Bruno

KeyWords Plus: BOTTLE-NOSED DOLPHINS; INDIVIDUAL RECOGNITION; TURSIOPS-TRUNCATUS; SIGNATURE WHISTLES; NONHUMAN-PRIMATES; RHESUS-MONKEY; ACOUSTIC CUES; VOCALIZATIONS; COMMUNICATION; IDENTITY

Abstract: Bouts of vocalizations given by seven red deer stags were recorded over the rutting period, and homomorphic analysis and hidden Markov models (two techniques typically used for the automatic recognition of human speech utterances) were used to investigate whether the spectral envelope of the calls was individually distinctive. Bouts of common roars (the most common call type) were highly individually distinctive, with an average recognition percentage of 93.5%. A "temporal" split-sample approach indicated that although in most individuals these identity cues held over the rutting period, the ability of the models trained with the bouts of roars recorded early in the rut to correctly classify later vocalizations decreased as the recording date increased. When Markov models trained using the bouts of common roars were used to classify other call types according to their individual membership, the classification results indicated that the cues to identity contained in the common roars were also present in the other call types. This is the first demonstration in mammals other than primates that individuals have vocal cues to identity that are common to the different call types that compose their vocal repertoire. (c) 2006 Acoustical Society of America.

Times Cited: 11

Record 10 of 12

McElligott, AG; Birrer, M; Vannoni, E. 2006. Retraction of the mobile descended larynx during groaning enables fallow bucks (Dama dama) to lower their formant frequencies. *JOURNAL OF ZOOLOGY* 270 (2): 340-345..

Author Full Name(s): McElligott, A. G.; Birrer, M.; Vannoni, E.

Author Keywords: body size; red deer; signalling; vocal communication; vocal tract

KeyWords Plus: VOCAL-TRACT LENGTH; RED DEER STAGS; REPRODUCTIVE EFFORT; MATING SUCCESS; BODY-SIZE; VOCALIZATION; COMMUNICATION; SOUNDS; CUES; AGE

Abstract: A permanently descended larynx is found in humans and several other species of mammals. In addition to this, the larynx of species such as fallow deer is mobile and in males it can be retracted during vocalization. The most likely explanation for the lowered retractable larynx in mammals is that it serves to exaggerate perceived body size (size exaggeration hypothesis) by decreasing the formant frequencies of calls. In this study, we quantified for the first time the elongation of the vocal tract in fallow bucks during vocalization. We also measured the effect of this vocal tract length (VTL) increase on formant frequencies (vocal tract resonances) and formant dispersion (spacing of formants). Our results show that fallow bucks increase their VTL on average by 52% during vocalization. This elongation resulted in strongly lowered formant frequencies and decreased formant dispersion. There were minimal changes to formants 1 and 2 (-0.91 and +1.9%, respectively) during vocal tract elongation, whereas formants 3, 4 and 5 decreased substantially: 18.9, 10.3 and 13.6%, respectively. Formant dispersion decreased by 12.4%. Formants are prominent in deer vocalizations and are used by males to gain information on the competitive abilities of signallers. It remains to be seen whether females also use the information that formants contain for assessing male quality before mating.

Times Cited: 14

Record 11 of 12

Reby, D; McComb, K; Cargnelutti, B; Darwin, C; Fitch, WT; Clutton-Brock, T. 2005. Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *PROCEEDINGS OF THE ROYAL SOCIETY B-BIOLOGICAL SCIENCES* 272 (1566): 941-947..

Author Keywords: red deer; vocal communication; formant frequencies; nonlinear phenomena

KeyWords Plus: VOCAL-TRACT LENGTH; CERVUS-ELAPHUS; EVOLUTION; FREQUENCY; BABOONS; SPEECH; CALLS

Abstract: While vocal tract resonances or formants are key acoustic parameters that define differences between phonemes in human speech, little is known about their function in animal communication. Here, we used playback experiments to present red deer stags with re-synthesized vocalizations in which formant frequencies were systematically altered to simulate callers of different body sizes. In response to stimuli where lower formants indicated callers with longer vocal tracts, stags were more attentive, replied with more roars and extended their vocal tracts further in these replies. Our results indicate that mammals other than humans use formants in vital vocal exchanges and can adjust their own formant frequencies in relation to those that they hear.

Times Cited: 56

Record 12 of 12

Reby, D; McComb, K. 2003. Vocal communication and reproduction in deer. *ADVANCES IN THE STUDY OF BEHAVIOR, VOL 33* 33: 231-264..

Book series title: ADVANCES IN THE STUDY OF BEHAVIOR

KeyWords Plus: WHITE-TAILED DEER; RED DEER; CERVUS-ELAPHUS; FALLOW BUCKS; DAMA-DAMA; RHESUS-MONKEY; MUNTIACUS-MUNTJAK; MACACA-MULATTA; TRACT LENGTH; BODY-SIZE

Times Cited: 25

NOTE: THIS IS NOT A DEFINITIVE LIST AND SHOULD ONLY BE USED FOR KEYWORDS/AUTHORS TO DO YOUR OWN SEARCH USING GOOGLE SCHOLAR AND WEB OF SCIENCE.

Record 1 of 17

Frey, R; Gebler, A; Olson, KA; Odonkhuu, D; Fritsch, G; Batsaikhan, N; Stuermer, IW. 2008. Mobile larynx in Mongolian gazelle: Retraction of the larynx during rutting barks in male Mongolian gazelle (Procapra gutturosa Pallas, 1777). *JOURNAL OF MORPHOLOGY* 269 (10): 1223-1237..

Author Full Name(s): Frey, Roland; Gebler, Alban; Olson, Kirk A.; Odonkhuu, Daria; Fritsch, Guido; Batsaikhan, Nyamsuren; Stuermer, Ingo W.

Author Keywords: vocal tract; comparative anatomy; laryngeal sound production; evolutionary morphology; rutting behavior

Keywords Plus: RED DEER STAGS; DESCENDED LARYNX; CERVUS-ELAPHUS; VOCAL-TRACT; REPRODUCTION; HANDICAP; BOVIDAE; HONESTY; ROARS; CUES

Abstract: This study provides the first evidence of pronounced temporary laryngeal descent in a bovid species. An elaborate acoustic display is prominent in male courtship behavior of polygynous Mongolian gazelle. During rut, rounding up of females is accompanied by continuous head-up barking by dominant males. Throughout the rut their evolutionarily enlarged larynx descends to a low mid-neck resting position. In the course of each bark the larynx is additionally retracted toward the sternum by 30% of the resting vocal tract length. A geometric model of active larynx movements was constructed by combining results of video documentation, dissection, skeletonization, and behavioral observation. The considerable distance between resting position and maximal laryngeal descent suggests a backward tilting of the hyoid apparatus and an extension of the thyrohyoid connection during the retraction phase. Return to the resting position is effected by strap muscles and by the elastic recoil of the pharynx and the thyrohyoid connection. An intrapharyngeal inflation of the peculiar palatinal pharyngeal pouch of adult males is inferred from a short-time expansion of the ventral neck region rostral to the laryngeal prominence. The neck of adult dominant males is accentuated by long gray guard hairs during the rut. The passive swinging of the heavy larynx of adult males during locomotion gives the impression of a handicap imposed on rutting males. Apparently, this disadvantage becomes outweighed by the profits for reproductive success.

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DOI: 10.1002/jmor.10656

Record 2 of 17

Charlton, BD; McComb, K; Reby, D. 2008. Free-ranging red deer hinds show greater attentiveness to roars with formant frequencies typical of young males. *ETHOLOGY* 114 (10): 1023-1031..

Author Full Name(s): Charlton, Benjamin D.; McComb, Karen; Reby, David

Keywords Plus: MONKEYS CERCOPITHECUS-AETHIOPS; HUMANS HOMO-SAPIENS; VOCAL-TRACT LENGTH; MATE CHOICE; ACOUSTIC CLASSIFICATION; RHESUS MACAQUES; ALARM CALLS; DISCRIMINATION; VOWEL; HONEST

Abstract: Acoustic cues present in the reproductive calls of many animal species potentially encode important information about the caller. Here, we test the response of a free-ranging population of peri-oestrus red deer hinds to variation in a specific acoustic cue to body size in the male roar, the formant frequencies. Our results revealed: (1) that hinds showed greater overall attention (judged by longer looking responses and lower response latencies) to roars simulating males of sub-adult body size than to those simulating a large adult male and (2) that hinds without dependent offspring had greater looking responses to male roars and lower response latencies than hinds with dependent offspring to roars simulating sub-adult males. These findings indicate that free-ranging red deer hinds may use formants as acoustic cues to gauge the body size and maturity of males in their natural environment, possibly to facilitate earlier detection and avoidance of young stags that are known to harass them.

Times Cited: 0

ISSN: 0179-1613

DOI: 10.1111/j.1439-0310.2008.01539.x

Record 4 of 17

Taylor, AM; Reby, D; McComb, K. 2008. Human listeners attend to size information in domestic dog growls. *JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA* 123 (5): 2903-2909, Part 1..

Author Full Name(s): Taylor, Anna M.; Reby, David; McComb, Karen

Keywords Plus: VOCAL-TRACT LENGTH; RED DEER STAGS; BODY-SIZE; SPEAKER HEIGHT; WEIGHT IDENTIFICATION; FORMANT FREQUENCIES; CANIS-FAMILIARIS; RHESUS MACAQUES; CUES; COMMUNICATION

Abstract: The acoustic features of vocalizations have the potential to transmit information about the size of callers. Most acoustic studies have focused on intraspecific perceptual abilities, but here, the ability of humans to use growls to assess the size of adult domestic dogs was tested. In a first experiment, the formants of growls were shifted to create playback stimuli with different formant dispersions (Delta f), simulating different vocal tract lengths within the natural range of variation. Mean fundamental frequency (F0) was left unchanged and treated as a covariate. In a second experiment, F0 was resynthesized and Af was left unchanged. In both experiments Delta f and F0 influenced how participants rated the size of stimuli. Lower formant and fundamental frequencies were rated as belonging to larger dogs. Crucially, when F0 was manipulated and Delta f was natural, ratings were strongly correlated with the actual weight of the dogs, while when Delta f was varied and F0 was natural, ratings were not related to the actual weight. Taken together, this suggests that participants relied more heavily on Delta f, in accordance with the fact that formants are better predictors of body size than F0. (c) 2008 Acoustical Society of America.

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ISSN: 0001-4966

DOI: 10.1121/1.2896962

Record 5 of 17

Charlton, BD; Reby, D; McComb, K. 2008. Effect of combined source (F0) and filter (formant) variation on red deer hind responses to male roars. *JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA* 123 (5): 2936-2943, Part 1..

Author Full Name(s): Charlton, Benjamin D.; Reby, David; McComb, Karen

Keywords Plus: VOCAL-TRACT LENGTH; BODY-SIZE; SEXUAL SELECTION; MATE CHOICE; ACOUSTIC ALLOMETRY; DESCENDED LARYNX; CERVUS-ELAPHUS; DAMA-DAMA; EVOLUTION; FREQUENCY

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Times Cited: 1

ISSN: 0001-4966

DOI: 10.1121/1.2896758

Record 7 of 17

Frey, R; Volodin, I; Volodina, E. 2007. A nose that roars: anatomical specializations and behavioural features of rutting male saiga. *JOURNAL OF ANATOMY* 211 (6): 717-736..

Author Full Name(s): Frey, Roland; Volodin, Ilya; Volodina, Elena

Author Keywords: acoustic communication; comparative anatomy; evolutionary morphology; formant analysis; larynx; mating system; rutting calls; Saiga tatarica; sexual selection; vocal tract

Keywords Plus: SEAL CYSTOPHORA-CRISTATA; NONHUMAN VOCAL TRACTS; RED DEER STAGS; VOMERONASAL ORGAN; MALE GOATS; BODY-SIZE; LARYNGEAL

ANATOMY; NARIAL ANATOMY; ACOUSTIC CUES; BOVIDAE

Abstract: The involvement of the unique saiga nose in vocal production has been neglected so far. Rutting male saigas produce loud nasal roars. Prior to roaring, they tense and extend their noses in a highly stereotypic manner. This change of nose configuration includes dorsal folding and convex curving of the nasal vestibulum and is maintained until the roar ends. Red and fallow deer males that orally roar achieve a temporary increase of vocal tract length (vtl) by larynx retraction. Saiga males attain a similar effect by pulling their flexible nasal vestibulum rostrally, allowing for a temporary elongation of the nasal vocal tract by about 20%. Decrease of formant frequencies and formant dispersion, as acoustic effects of an increase of vtl, are assumed to convey important information on the quality of a dominant male to conspecifics, e.g. on body size and fighting ability. Nasal roaring in saiga may equally serve to deter rival males and to attract females. Anatomical constraints might have set a limit to the rostral pulling of the nasal vestibulum. It seems likely that the sexual dimorphism of the saiga nose was induced by sexual selection. Adult males of many mammalian species, after sniffing or licking female urine or genital secretions, raise their head and strongly retract their upper lip and small nasal vestibulum while inhalating orally. This flehmen behaviour is assumed to promote transport of non-volatile substances via the incisive ducts into the vomeronasal organs for pheromone detection. The flehmen aspect in saiga involves the extensive flexible walls of the greatly enlarged nasal vestibulum and is characterized by a distinctly concave configuration of the nose region, the reverse of that observed in nasal roaring. A step-by-step model for the gradual evolution of the saiga nose is presented here.

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ISSN: 0021-8782

DOI: 10.1111/j.1469-7580.2007.00818.x

Record 8 of 17

Charlton, BD; Reby, D; McComb, K. 2007. Female perception of size-related formant shifts in red deer, Cervus elaphus. *ANIMAL BEHAVIOUR* 74: 707-714, Part 4..

Author Full Name(s): Charlton, Benjamin D.; Reby, David; McComb, Karen

Author Keywords: acoustic cues; body size; Cervus elaphus; formant frequency; perception; red deer; vocal communication

Keywords Plus: VOCAL-TRACT LENGTH; ACOUSTIC STRUCTURE; RHESUS MACAQUES; MONKEYS CERCOPITHECUS; PLAYBACK EXPERIMENTS; GRUNT VOCALIZATIONS; SPEECH-PERCEPTION; MACACA-MULATTA; VERVET MONKEYS; DISCRIMINATION

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simulate the other size variant. The signficant reduction in behavioural response to final rehabituation playback showed this was not a chance rebound in response levels. Our results suggest that formants are salient for red deer hinds and that hinds can detect a shift in formant frequencies that may have biological significance. We discuss the possible functions of formant perception in female red deer and more generally in nonhuman mammals.

Times Cited: 2

ISSN: 0003-3472

DOI: 10.1016/j.anbehav.2006.09.021

Record 10 of 17

Charlton, BD; Reby, D; McComb, K. 2007. Female red deer prefer the roars of larger males. *BIOLOGY LETTERS* 3 (4): 382-385..

Author Full Name(s): Charlton, Benjamin D.; Reby, David; McComb, Karen

Author Keywords: red deer; female mating preferences; vocal communication; formant frequencies; acoustic cues to body size

Keywords Plus: VOCAL-TRACT LENGTH; ACOUSTIC STRUCTURE; CERVUS-ELAPHUS; MATE CHOICE; VOCALIZATION; STAGS; INFORMATION; CUES

Abstract: Surprisingly little is known about the role of acoustic cues in mammal female mate choice. Here, we examine the response of female red deer (Cervus elaphus) to male roars in which an acoustic cue to body size, the formants, has been re-scaled to simulate different size callers. Our results show that oestrous red deer hinds prefer roars simulating larger callers and constitute the first evidence that female mammals use an acoustic cue to body size in a mate choice context. We go on to suggest that 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.

Times Cited: 6

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Author Full Name(s): Vannoni, Elisabetta; McElligott, Alan G.

Keywords Plus: VOICE PERTURBATION MEASUREMENTS; VOCAL-TRACT LENGTH; BABOON LOUD CALLS; RED DEER; DISCRIMINANT-ANALYSIS; DESCENDED LARYNX; MATING SUCCESS; CERVUS-ELAPHUS; ALARM CALLS; ROE DEER

Abstract: Mammals are able to distinguish conspecifics based on vocal cues, and the acoustic structure of mammal vocalizations is directly affected by the anatomy and action of the vocal apparatus. However, most studies investigating individual patterns in acoustic signals do not

consider a vocal production-based perspective. In this study, we used the source-filter model of vocal production as a basis for investigating the acoustic variability of fallow deer groans. Using this approach, we quantified the potential of each acoustic component to carry information about individual identity. We also investigated if cues to individual identity carry over among the two groan types we describe: common and harsh groans. Using discriminant function analysis, we found that variables related to the fundamental frequency contour and the minimum frequencies of the highest formants contributed most to the identification of a given common groan. Common groans were individually distinctive with 36.6% (53.6% with stepwise procedure) of groans assigned to the correct individual. This level of discrimination is approximately six times higher than that predicted by chance. In addition, univariate ANOVAS showed significant inter-individual variation in the minimum formant frequencies when common and harsh groans were combined, suggesting that some information about individuality is shared between groan types. Our results suggest that the sound source and the vocal tract resonances act together to determine groan individuality and that enough variation exists to potentially allow individual recognition based on groans.

Times Cited: 5

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DOI: 10.1111/j.1439-0310.2006.01323.x

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Frey, R; Gebler, A; Fritsch, G; Nygren, K; Weissengruber, GE. 2007. Nordic rattle: the hoarse vocalization and the inflatable laryngeal air sac of reindeer (Rangifer tarandus). *JOURNAL OF ANATOMY* 210 (2): 131-159..

Author Full Name(s): Frey, Roland; Gebler, Alban; Fritsch, Guido; Nygren, Kaarlo; Weissengruber, Gerald E.

Author Keywords: acoustic communication; air sac; comparative anatomy; courtship behaviour; larynx; reindeer; sound production

Keywords Plus: PROCAPRA-GUTTUROSA PALLAS; RED DEER STAGS; FALLOW BUCKS; HONEST ADVERTISEMENT; RUTTING BEHAVIOUR; DESCENDED LARYNX; VOCAL-TRACT; DAMA-DAMA; BODY-SIZE; BOVIDAE

Abstract: Laryngeal air sacs have evolved convergently in diverse mammalian lineages including insectivores, bats, rodents, pinnipeds, ungulates and primates, but their precise function has remained elusive. Among cervids, the vocal tract of reindeer has evolved an unpaired inflatable ventrorostral laryngeal air sac. This air sac is not present at birth but emerges during ontogenetic development. It protrudes from the laryngeal vestibulum via a short duct between the epiglottis and the thyroid cartilage. In the female the growth of the air sac stops at the age of 2-3 years, whereas in males it continues to grow up to the age of about 6 years, leading to a pronounced sexual dimorphism of the air sac. In adult females it is of moderate size (about 100 cm(3)), whereas in adult males it is large (3000-4000 cm(3)) and becomes asymmetric extending either to the left or to the right side of the neck. In both adult females and males the ventral air sac walls touch the integument. In the adult male the air sac is laterally covered by the

mandibular portion of the sternocephalic muscle and the skin. Both sexes of reindeer have a double stylohyoid muscle and a thyroepiglottic muscle. Possibly these muscles assist in inflation of the air sac. Head-and-neck specimens were subjected to macroscopic anatomical dissection, computer tomographic analysis and skeletonization. In addition, isolated larynges were studied for comparison. Acoustic recordings were made during an autumn round-up of semi-domestic reindeer in Finland and in a small zoo herd. Male reindeer adopt a specific posture when emitting their serial hoarse rutting calls. Head and neck are kept low and the throat region is extended. In the ventral neck region, roughly corresponding to the position of the large air sac, there is a mane of longer hairs. Neck swelling and mane spreading during vocalization may act as an optical signal to other males and females. The air sac, as a side branch of the vocal tract, can be considered as an additional acoustic filter. Individual acoustic recognition may have been the primary function in the evolution of a size-variable air sac, and this function is retained in mother-young communication. In males sexual selection seems to have favoured a considerable size increase of the air sac and a switch to call series instead of single calls. Vocalization became restricted to the rutting period serving the attraction of females. We propose two possibilities for the acoustic function of the air sac in vocalization that do not exclude each other. The first assumes a coupling between air sac and the environment, resulting in an acoustic output that is a combination of the vocal tract resonance frequencies emitted via mouth and nostrils and the resonance frequencies of the air sac transmitted via the neck skin. The second assumes a weak coupling so that resonance frequencies of the air sac are lost to surrounding tissues by dissipation. In this case the resonance frequencies of the air sac solely influence the signal that is further filtered by the remaining vocal tract. According to our results one acoustic effect of the air sac in adult reindeer might be to mask formants of the vocal tract proper. In other cervid species, however, formants of rutting calls convey essential information on the quality of the sender, related to its potential reproductive success, to conspecifics. Further studies are required to solve this inconsistency.

Times Cited: 2

ISSN: 0021-8782

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Reby, D; Andre-Obrecht, R; Galinier, A; Farinas, J; Cargnelutti, B. 2006. Cepstral coefficients and hidden Markov models reveal idiosyncratic voice characteristics in red deer (Cervus elaphus) stags. *JOURNAL OF THE ACOUSTICAL SOCIETY OF AMERICA* 120 (6): 4080-4089..

Author Full Name(s): Reby, David; Andre-Obrecht, Regine; Galinier, Arnaud; Farinas, Jerome; Cargnelutti, Bruno

Keywords Plus: BOTTLE-NOSED DOLPHINS; INDIVIDUAL RECOGNITION; TURSIOPS-TRUNCATUS; SIGNATURE WHISTLES; NONHUMAN-PRIMATES; RHESUS-MONKEY; ACOUSTIC CUES; VOCALIZATIONS; COMMUNICATION; IDENTITY

Abstract: Bouts of vocalizations given by seven red deer stags were recorded over the rutting

period, and homomorphic analysis and hidden Markov models (two techniques typically used for the automatic recognition of human speech utterances) were used to investigate whether the spectral envelope of the calls was individually distinctive. Bouts of common roars (the most common call type) were highly individually distinctive, with an average recognition percentage of 93.5%. A "temporal" split-sample approach indicated that although in most individuals these identity cues held over the rutting period, the ability of the models trained with the bouts of roars recorded early in the rut to correctly classify later vocalizations decreased as the recording date increased. When Markov models trained using the bouts of common roars were used to classify other call types according to their individual membership, the classification results indicated that the cues to identity contained in the common roars were also present in the other call types. This is the first demonstration in mammals other than primates that individuals have vocal cues to identity that are common to the different call types that compose their vocal repertoire. (c) 2006 Acoustical Society of America.

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Author Full Name(s): McElligott, A. G.; Birrer, M.; Vannoni, E.

Author Keywords: body size; red deer; signalling; vocal communication; vocal tract

Keywords Plus: VOCAL-TRACT LENGTH; RED DEER STAGS; REPRODUCTIVE EFFORT; MATING SUCCESS; BODY-SIZE; VOCALIZATION; COMMUNICATION; SOUNDS; CUES; AGE

Abstract: A permanently descended larynx is found in humans and several other species of mammals. In addition to this, the larynx of species such as fallow deer is mobile and in males it can be retracted during vocalization. The most likely explanation for the lowered retractable larynx in mammals is that it serves to exaggerate perceived body size (size exaggeration hypothesis) by decreasing the formant frequencies of calls. In this study, we quantified for the first time the elongation of the vocal tract in fallow bucks during vocalization. We also measured the effect of this vocal tract length (VTL) increase on formant frequencies (vocal tract resonances) and formant dispersion (spacing of formants). Our results show that fallow bucks increase their VTL on average by 52% during vocalization. This elongation resulted in strongly lowered formant frequencies and decreased formant dispersion. There were minimal changes to formants 1 and 2 (-0.91 and +1.9%, respectively) during vocal tract elongation, whereas formants 3, 4 and 5 decreased substantially: 18.9, 10.3 and 13.6%, respectively. Formant dispersion decreased by 12.4%. Formants are prominent in deer vocalizations and are used by males to gain information on the competitive abilities of signallers. It remains to be seen whether females also use the information that formants contain for assessing male quality before mating.

Times Cited: 4

ISSN: 0952-8369

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Author Keywords: red deer; vocal communication; formant frequencies; nonlinear phenomena

Keywords Plus: VOCAL-TRACT LENGTH; CERVUS-ELAPHUS; EVOLUTION; FREQUENCY; BABOONS; SPEECH; CALLS

Abstract: While vocal tract resonances or formants are key acoustic parameters that define differences between phonemes in human speech, little is known about their function in animal communication. Here, we used playback experiments to present red deer stags with re-synthesized vocalizations in which formant frequencies were systematically altered to simulate callers of different body sizes. In response to stimuli where lower formants indicated callers with longer vocal tracts, stags were more attentive, replied with more roars and extended their vocal tracts further in these replies. Our results indicate that mammals other than humans use formants in vital vocal exchanges and can adjust their own formant frequencies in relation to those that they hear.

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