

Retraction of the mobile descended larynx during groaning enables fallow bucks (*Dama dama*) to lower their formant frequencies

A. G. McElligott, M. Birrer & E. Vannoni

Zoologisches Institut, Universität Zürich, Zürich, Switzerland

Keywords

body size; red deer; signalling; vocal communication; vocal tract.

Correspondence

Alan G. McElligott, Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstr. 190, CH-8057 Zürich, Switzerland. Tel: +41 44 6355486; Fax: +41 44 6355490
Email: amcellig1@yahoo.ie

Received 11 August 2005; accepted 14 February 2006

doi:10.1111/j.1469-7998.2006.00144.x

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.

Introduction

Recent research has shown that a descended larynx in mammals is more widespread than previously believed, and is not restricted to humans (Fitch & Reby, 2001; Weissengruber *et al.*, 2002). Humans *Homo sapiens*, for example, have a permanently descended larynx; it moves from its high intranarial location down into the throat between 3 months and 3 years of age. There is a secondary descent of the larynx that occurs at puberty and is restricted to males (Fitch & Giedd, 1999). In addition to being descended, the larynx of red deer stags *Cervus elaphus* and fallow bucks is mobile and can be retracted even further during vocalization by the sterno-thyroid and sterno-hyoid muscles. This increases the vocal tract length (VTL) and results in lower formant frequencies (vocal tract resonances) and formant dispersion (spacing of formants) (Fitch, 2000a; Fitch & Reby, 2001; Weissengruber *et al.*, 2002; Reby & McComb, 2003a,b).

There are a number of hypotheses that have been used to explain the evolution of the permanently descended larynx. Lieberman, Klatt & Wilson (1969) suggested that a low larynx allows humans to create a wider range of vocal tract shapes, and thus more varied and distinctive speech sounds than other mammals. Thus, lowering of the larynx has been considered a key point in the evolution of the spoken human

language. However, there are many non-speaking species, which possess a descended and/or retractable larynx (Sonntag, 1921; Fitch, 2000a; Fitch & Reby, 2001; Weissengruber *et al.*, 2002). Other hypotheses propose that the laryngeal lowering was a non-adaptive by-product of upright posture or it could be adaptive for mouth breathing during extreme physical challenge (Dubrul, 1976; Lieberman, 1984). Moreover, laryngeal lowering could also increase the effectiveness with which calls propagate through the environment by enhancing the low-frequency components (Morton, 1975; Michelsen, 1978; Wiley & Richards, 1982).

The evolution of the descended larynx, particularly in males of several independent lineages (e.g. cats, deer, humans), suggests that it could be related to the signalling of competitive abilities (Hauser, 1996; Fitch & Reby, 2001; Seyfarth & Cheney, 2003). In humans, macaques *Macaca mulatta* and dogs *Canis familiaris*, body size and VTL are positively related to one another (Fitch, 1997, 2000b; Fitch & Giedd, 1999; Riede & Fitch, 1999). VTL is also directly related to formant frequencies (Fitch & Reby, 2001). Therefore, Fitch & Reby (2001) proposed that the descended larynx in deer serves to give receivers an exaggerated impression of body size (size exaggeration hypothesis) by decreasing the formant frequencies and formant dispersion of calls. The resulting change in perceived body size could

have increased the chances that males would attract mates and/or deter competitors. Nevertheless, the minimum formant frequencies, achieved when the larynx is fully pulled down to the sternum, still provide an honest indication of body size (Reby & McComb, 2003a). This is because the sternum acts as a morphological constraint, beyond which further retraction of the larynx is not possible. Additional support for the size exaggeration hypothesis comes from playback experiments on red deer males. Red deer males use formants to assess other males during roaring contests and can adjust their own formant frequencies in relation to those that they hear (Reby *et al.*, 2005).

Fallow bucks only vocalize during the breeding season. They start groaning in late September and produce a low-pitched, stereotyped and repetitive call ranging from 20 to 8000 Hz (Reby *et al.*, 1998; McElligott, O'Neill & Hayden, 1999; Fitch & Reby, 2001; Vannoni, Torriani & McElligott, 2005). One groan lasts on average 0.3–0.5 s and is composed of regularly spaced pulses, which are produced by vibrations of the vocal cords (Reby *et al.*, 1998). Fallow bucks modify their vocal tract during calling by pulling the larynx down towards the sternum (Fitch & Reby, 2001).

Male deer that are able to retract their larynges further than average, and thus lower their formant frequencies and increase their perceived body size, would have advantages in intrasexual competition and intersexual advertisement (Fitch, 2002; Reby *et al.*, 2005). In this study, we quantify for the first time the elongation of the vocal tract in fallow bucks during vocalization. We also measure the effect of this VTL increase on formant frequencies and formant dispersion.

Methods

Study site and study population

This study was carried out in Phoenix Park, Dublin, Ireland. It is a large enclosed city park (709 ha, 20% open woodland, 80% pasture), situated 2.4 km west of the centre of Dublin (53°22'N, 6°21'W).

Audio and video recordings

We carried out audio and video recordings of mature, groaning fallow bucks (≥ 4 years old; McElligott *et al.*, 1998) from 12 October to 29 October 2003. We used a directional microphone (Sennheiser MKH-70; Old Lyme, CT, USA) plugged into a digital video camera (Sony, DCR-TRV50E; Tokyo, Japan). In other cases we recorded the audio and video sequences separately with the video camera and a digital audio tape recorder (Sony, TCD-D100) connected to the directional microphone. The recorded animals were between 20 and 100 m away from the microphone and at an angle of *c.* 90° to the video camera. After each recording session, we recorded a meter stick at the same location as the male ($n = 7$ males). Distances were measured using a Leica rangefinder (Leica Camera AG, Solms, Germany). During picture analysis, we used this recorded

meter stick to obtain a suitable reference for converting the pixels into centimetres.

Body measurements

On 23 September, one male was caught and some body measurements were taken (for details of the capture method, see McElligott *et al.*, 2001). These were the distance from the pre-orbital gland to the tip of the nose, on both sides of the head. This facial measurement was also taken from two males that died just after the breeding season, in November. The facial measurements also served as references, which were crucial to convert pixels into centimetres, for the three remaining males (total $n = 10$; see Results).

VTL measurements and changes during groaning

All pictures needed for VTL measurements were extracted from video sequences using Pinnacle Studio Version 8. We measured the position of the larynx on the pictures using Scion Image Beta Version 4.0.2 (available from www.scion-corp.com). VTL was measured as the distance from the tip of the snout to the larynx. We converted this value from pixels into centimetres using the meter stick or the facial measurements (Fitch & Reby, 2001).

The minimum VTL was measured three times on three different pictures for each male ($n = 10$). Therefore, the minimum VTL (when the larynx was in the resting position) was calculated as the mean of nine measurements. It should be more or less a fixed value for a male, because this is when the males are not groaning and the larynx is in the resting position. We also measured the maximum VTL (when the larynx was retracted) for each groan in the same way. Finally, it was possible to measure the distance from the tip of the snout to the sternum for four males, and again we used the mean of nine measurements.

We measured the VTL at the pre-groan stage (when the males were not groaning), at the onset of vocalizing, and when the larynx was fully pulled down. We compared the change in formant frequencies and formant dispersion over those three stages ('three-frame groan analysis'; Fig. 1). We used the frequencies and VTL measurements of one to seven groans from nine males (four males, four groans; two males, five groans; three males, one, three and seven groans, respectively).

Acoustic analysis

We extracted the audio files from the video sequences using Pinnacle Studio Version 8. The sample rate of the extracted original recordings was 48 000 Hz. Formant frequencies were measured using linear predictive coding analysis (Press *et al.*, 1992) with Praat 4.2 (available from Paul Boersma & David Weenink, www.praat.org). We used formants 3, 4 and 5 (F_3 – F_5) for our detailed analyses. The first two formants (F_1 , F_2) were usually flat and these are simply reported. It is assumed that the F_1 and F_2 frequencies are absorbed by the vocal tract and that this is the reason for the

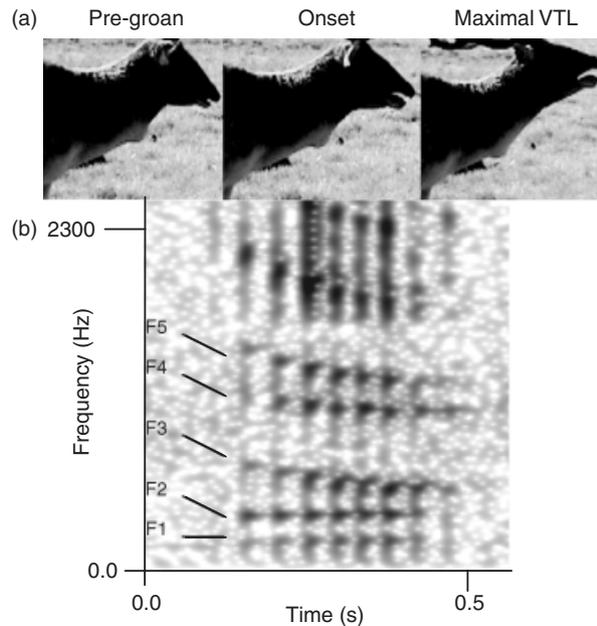


Figure 1 (a) Photos taken from videotape of a fallow buck groaning once [vocal tract length (VTL) increase over the three stages: pre-groan, onset and maximal VTL]; (b) spectrogram of the emitted groan, showing decreasing formant frequencies of five clearly detectable formants during groaning.

flat appearance in the spectrogram (Fig. 1; W. T. Fitch, pers. comm.). The parameters were set as follows: maximum formant, 2000 Hz; maximum number of formants, 6–14; window length, 0.1 or 0.2 s; time step, 0.04 s. We calculated formant dispersion (D_f) according to Reby & McComb (2003a).

Relationship between VTL and formants (F_3 – F_5 , formant dispersion)

We carried out a framewise analysis of formant frequencies, formant dispersion and VTL during groaning (frame window = 0.04 s). We used measurements of 1–11 groans from nine males (three males, six groans; two males, eight groans; four males, one, five, seven and 11 groans, respectively).

Statistical analysis

All statistical analyses were performed using R for Windows version 2.0.1 (R Development Core Team, 2004): the packages 'nlme' (Pinheiro *et al.*, 2004) and 'MASS' (Venables & Ripley, 2002). All tests are two-tailed and factors were considered to have a statistically significant influence if $P < 0.05$. All means are given with standard errors. To determine the relationship between increasing VTL and formant frequencies, we used a linear mixed effects model procedure fitted with residual maximum likelihood estimation (REML, lme function; Venables & Ripley 2002). The number of groans nested within individual identity was

Table 1 Minimum vocal tract length (VTL), maximum VTL, absolute VTL increase and percentage VTL increase for each male ($n = 10$)

Male	Age (years)	Minimum VTL	Maximum VTL	VTL increase	VTL increase (%)
b309	5	32.0 ± 0	46.7 ± 0.58	18.7 ± 0.58	45.9
y736	6	34.0 ± 0.5	54.3 ± 4.15	20.3 ± 4.15	59.7
y717	6	33.6 ± 1.51	53.3 ± 1.26	19.7 ± 1.26	58.6
y746	6	32.2 ± 1.09	50.0 ± 0	17.8 ± 0	55.3
y693	6	32.1 ± 0.78	48.4 ± 2.07	16.3 ± 2.07	50.8
y747	6	32.9 ± 0.33	48.0 ± 1.5	15.1 ± 0	45.9
w433	7	31.2 ± 2.17	48.0 ± 1.83	16.8 ± 1.83	53.8
w591	7	28.8 ± 0.97	46.4 ± 1.67	18.1 ± 1.67	61.1
w504	7	32.2 ± 0.67	46.0 ± 1.41	13.8 ± 1.41	42.9
g477	8	33.3 ± 1	48.5 ± 1	15.2 ± 1	45.6

The mean maximum VTL and the mean increase in VTL were calculated using 40 groans. All lengths are given in cm.

fitted as a random term. In this way, we controlled for repeated sampling within individuals. Formant frequencies and formant dispersion were fitted as fixed effects. We checked our data to verify that the assumptions of residual normality and variance homoscedasticity were satisfied. Good video recordings were available for 10 males (results in Table 1). However acoustic analyses were conducted for nine males because there were no good quality sound recordings for one male (remaining results).

Results

Change in VTL during groaning

The data for mean minimum VTL, maximum VTL, absolute VTL increase and percentage increase of VTL for 10 males are given in Table 1. These were measured from the images of the vocalizing males. The overall mean minimum VTL was 32.2 ± 1.5 cm, range 28.8–34 cm. The overall mean maximum VTL was 49.0 ± 2.8 cm, range 44–59 cm. The males increased their VTL on average by 17.5 ± 2.9 cm, range 13.8–20.3 cm (Table 1). This represents an overall percentage increase in VTL of 52.0 ± 6.7%, range 42.9–61.1% (Table 1).

For the four males for which we could measure the distance from the tip of the snout to the sternum, the overall mean was 75.1 ± 6.6 cm, range 63–85 (w433 = 66.3 ± 2.1 cm, g477 = 73.8 ± 1.9 cm, y717 = 81.1 ± 3.8 cm, y736 = 79.2 ± 2.7 cm). Therefore, the maximum VTL that these males attained represented 68.1 ± 3.1% of the distance between the tip of the snout and sternum.

Relationship between VTL and formants (F_3 – F_5 , formant dispersion)

For the nine males for which we had good sound recordings, the VTL increased by 54.0% (Table 2). There were minimal changes in F_1 (–0.91%) and F_2 (+1.9%) during vocal tract elongation, whereas F_3 decreased by 18.9%, F_4 by 10.3%

Table 2 Vocal tract length (VTL), frequencies of the first five formants (F_1 – F_5) and formant dispersion (D_i) as the larynx descends during vocalizing

	VTL (cm)	Formant frequencies (Hz)					D_i
		F_1	F_2	F_3	F_4	F_5	
A	32.2 ± 2.2	–	–	–	–	–	–
B	32.9 ± 2.0	220.4 ± 22.1	404.8 ± 31.7	708.5 ± 44.9	1183.1 ± 48.2	1458.4 ± 105.5	319.8 ± 16.5
C	49.6 ± 3.7	218.4 ± 20.6	412.4 ± 19.8	574.7 ± 50.1	1061.7 ± 37.0	1259.7 ± 46.1	280.0 ± 9.9

A, VTL at rest (pre-groan); B, minimum VTL during the groan (measured at the onset of vocalizing); C, maximum VTL during the groan ($n=37$ groans, $n=9$ males).

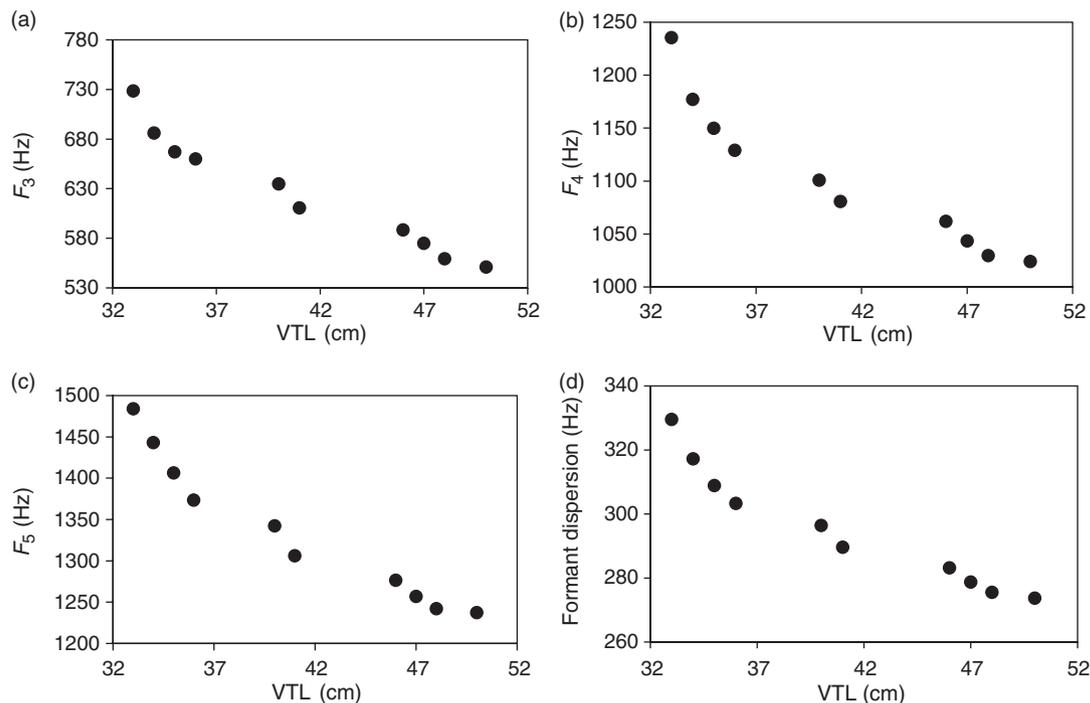


Figure 2 Relationship between increasing vocal tract length (VTL) and (a) formant 3, (b) formant 4, (c) formant 5 and (d) formant dispersion. The example is taken from a single groan of one male ($n=10$ frames).

and F_5 by 13.6% (Table 2). Formant dispersion decreased by 12.4% (Table 2).

The framewise analysis revealed a strong negative relationship between formant frequencies and the location of the larynx (VTL), and also between formant dispersion and VTL. F_3 – F_5 and formant dispersion decreased significantly with increasing VTL (linear mixed effect model: F_3 , $F_{1,536} = 2448.5$; F_4 , $F_{1,547} = 1913.7$; F_5 , $F_{1,540} = 1792.3$; formant dispersion, $F_{1,523} = 2838.2$; $P < 0.0001$ in all cases). The negative relationships between formant frequencies, formant dispersion and VTL are illustrated using one groan from one male in Fig. 2.

Discussion

Our results show that fallow bucks increase their VTL on average by 52% during vocalization, and the maximum VTL that some males attained was 65% of the distance between the tip of the snout and sternum. This elongation

resulted in lowered formants (vocal tract resonances) and consequently decreased formant dispersion (spacing of formants). Most evidence suggests that the evolution of the descended larynx in cervids and other mammals occurred through 'size exaggeration', whereby males attempt to exaggerate their perceived body size by modifying the phonic structure of their calls (Fant, 1975; Fitch & Reby, 2001; Reby & McComb, 2003a,b). Recent research has also revealed that red deer stags use the formant frequencies of roars for assessing competitors during intrasexual competition and can adjust their own formants in relation to those of perceived rivals (Reby *et al.*, 2005).

Formants and formant dispersion are key features of calls because they are related to the length and shape of the supralaryngeal vocal tract and are related to body size (Fitch, 1997, 2000b; Riede & Fitch, 1999). Body size in turn is often related to male competitive abilities and reproductive success (Andersson, 1994; McElligott *et al.*, 2001). The role of formants in intersexual advertisement, and possibly

mate choice in deer, remains to be studied (Reby *et al.*, 2005). However, there is already evidence from humans showing that females prefer lower formant frequencies, because they are indicative of sexual maturity in males (Feinberg *et al.*, 2005). In humans, lower fundamental frequencies and/or increasing apparent VTLs of males increased female ratings of masculinity, size and age of the speaker (Feinberg *et al.*, 2005). In addition, Reby & McComb (2003a) showed that there was a strong relationship between the minimum formant frequencies (reached during the part of the roar when the larynx is most fully retracted towards the sternum) and reproductive success in red deer. This association of higher reproductive success with formant frequencies is likely to be achieved through both intersexual advertisement and intrasexual competition.

Increasing the VTL during vocalization results in lower formant frequencies (Fitch & Reby, 2001; this study). In general, lower frequency sounds travel further than higher frequency ones, because higher frequencies are affected more by the environment, and therefore the evolution of the mobile descended larynx could have resulted from the need to increase the effectiveness of sound propagation over longer distances (Morton, 1975; Michelsen, 1978; Wiley & Richards, 1982; Fitch & Reby, 2001). However, when calls are emitted close to the ground, as is the case in fallow and other deer species, there is a peak in attenuation in the 300–800 Hz range (Morton, 1975; Marten & Marler, 1977; Fitch & Reby, 2001). This is the frequency range that is also produced by the lowering of the larynx, and therefore increasing the distances over which calls are heard cannot explain its evolution. The movement of the larynx during vocalization and the resulting lowered formants may in fact reduce sound propagation (Fitch & Reby, 2001).

The increase in VTL of fallow bucks during calling, at 52% (this study), is far less than that of red deer stags (*c.* 100%; Fitch & Reby, 2001). In an earlier review it was noted that red deer stags usually pull down the larynx to its maximum level at the sternum for almost all roars. By contrast, in our study, we found that fallow bucks pull the larynx to 65% of the distance between the tip of the snout and the sternum. This was also noted in an earlier review by Reby & McComb (2003b). Roaring in red deer also begins when the larynx is already pulled down by 37% (Fitch & Reby, 2001), whereas groaning in fallow deer begins immediately with laryngeal descent (see Table 2). These important differences probably result from the very different rates at which these two species vocalize. Whereas fallow bucks commonly achieve groaning rates of 60 and over per minute, the maximum roaring rate of red deer stag is *c.* 8 min⁻¹ (Clutton Brock & Albon, 1979; McElligott & Hayden, 1999, 2001). Therefore, it suggests that achieving very high calling rates is more important for fallow deer than always lowering the larynx to its maximum level at the sternum, as in red deer.

Elongating the vocal tract in order to exaggerate their perceived body size would initially have been advantageous for males when this trait first started to evolve. However,

once all males can lower the larynx, the net benefit of this adaptation would be eliminated (Fitch & Reby, 2001). Both fallow bucks and red stags compete intensively for access to mating opportunities during the breeding season, and as a result they lose a great deal of body condition (Yoccoz *et al.*, 2002; McElligott *et al.*, 2003). The loss in body condition, particularly towards the end of the breeding season, could also affect the ability of a male to retract the larynx during vocalization, because it is likely that current energy reserves also affect the muscles responsible for retraction. Therefore, the relative abilities of males to reduce the formant frequencies of calls could potentially provide information on current body condition and competitive abilities. It is already known that fallow bucks are able to detect changes in the current condition of rival males (McElligott *et al.*, 1998), and vocalizations are likely to be one of the main routes through which this information is obtained.

This is the first time that the increase in the VTL during vocalization for fallow bucks has been measured, and its subsequent effect on the formant frequencies quantified. It is clear that formants form a very important component of the phonic structure of vocalizations that are used by males of some mammals to gain information on signallers (Fitch & Reby, 2001; Reby & McComb, 2003a; Reby *et al.*, 2005). Future research should examine if females also use the information that is contained in formants.

Acknowledgements

We thank Dr Tom Hayden, Billy Clarke and other members of the Mammal Research Group, University College Dublin for their assistance with fieldwork. We thank Dúchas The Heritage Service and the staff of Phoenix Park for their support. Thanks to Tecumseh Fitch for helpful advice during data collection and analysis and to David Reby for advice during preparation of the manuscript. We are grateful to Lorenz Gyax and Linda Hollén for help with the statistics. We acknowledge the financial support of Erasmus/Socrates (M. B.), the Forschungskommission der Universität Zürich (E. V.) and the Swiss Academy of Sciences (E. V.).

References

- Andersson, M. (1994). *Sexual selection*. New Jersey: Princeton University Press.
- Clutton Brock, T.H. & Albon, S.D. (1979). The roaring of red deer and the evolution of honest advertising. *Behaviour* **69**, 145–170.
- Dubrul, E.L. (1976). Biomechanics of speech sounds. *Ann. NY Acad. Sci.* **280**, 631–642.
- Fant, G. (1975). Non-uniform vowel normalization. *Speech Trans. Lab. Q. Progr. Status Rep.* **2–3**, 1–19.
- Feinberg, D.R., Jones, B.C., Little, A.C., Burt, D.M. & Perrett, D.I. (2005). Manipulations of fundamental and formant frequencies influence the attractiveness of human male voices. *Anim. Behav.* **69**, 561–568.

- Fitch, W.T. (1997). Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *J. Acoust. Soc. Am.* **102**, 1213–1222.
- Fitch, W.T. (2000a). The phonetic potential of nonhuman vocal tracts: comparative cineradiographic observations of vocalizing animals. *Phonetica* **57**, 205–218.
- Fitch, W.T. (2000b). Skull dimensions in relation to body size in nonhuman mammals: the causal bases for acoustic allometry. *Zoology* **103**, 40–58.
- Fitch, W.T. (2002). Comparative vocal production and the evolution of speech: reinterpreting the descent of the larynx. In *The transition to language*: 21–45. Wray, A. (Ed.). Oxford: Oxford University Press.
- Fitch, W.T. & Giedd, J. (1999). Morphology and development of the human vocal tract: a study using magnetic resonance imaging. *J. Acoust. Soc. Am.* **106**, 1511–1522.
- Fitch, W.T. & Reby, D. (2001). The descended larynx is not uniquely human. *Proc. Roy. Soc. Lond. Ser. B* **268**, 1669–1675.
- Hauser, M.D. (1996). *The evolution of communication*. Cambridge, MA: MIT Press.
- Lieberman, P. (1984). *The biology and evolution of language*. Cambridge, MA: Harvard University Press.
- Lieberman, P., Klatt, D.H. & Wilson, W.H. (1969). Vocal tract limitations on the vowel repertoires of rhesus monkeys and other nonhuman primates. *Science* **164**, 1185–1187.
- Marten, K. & Marler, P. (1977). Sound transmission and its significance for animal vocalization. 1. Temperate habitats. *Behav. Ecol. Sociobiol.* **2**, 271–290.
- McElligott, A.G., Gammell, M.P., Harty, H.C., Paini, D.R., Murphy, D.T., Walsh, J.T. & Hayden, T.J. (2001). Sexual size dimorphism in fallow deer: do larger, heavier males gain greater mating success? *Behav. Ecol. Sociobiol.* **49**, 266–272.
- McElligott, A.G. & Hayden, T.J. (1999). Context-related vocalization rates of fallow bucks, *Dama dama*. *Anim. Behav.* **58**, 1095–1104.
- McElligott, A.G. & Hayden, T.J. (2001). Postcopulatory vocalizations of fallow bucks: who is listening? *Behav. Ecol.* **12**, 41–46.
- McElligott, A.G., Mattiangeli, V., Mattiello, S., Verga, M., Reynolds, C.A. & Hayden, T.J. (1998). Fighting tactics of fallow bucks (*Dama dama*, Cervidae): reducing the risks of serious conflict. *Ethology* **104**, 789–803.
- McElligott, A.G., Naulty, F., Clarke, W.V. & Hayden, T.J. (2003). The somatic cost of reproduction: what determines reproductive effort in prime-aged fallow bucks? *Evol. Ecol. Res.* **5**, 1239–1250.
- McElligott, A.G., O'Neill, K.P. & Hayden, T.J. (1999). Cumulative long-term investment in vocalization and mating success of fallow bucks, *Dama dama*. *Anim. Behav.* **57**, 1159–1167.
- Michelsen, A. (1978). Sound reception in different environments. In *Sensory ecology: review and perspectives*: 345–373. Ali, M. (Ed.). New York: Plenum Press.
- Morton, E.S. (1975). Ecological sources of selection on avian sounds. *Am. Nat.* **109**, 17–34.
- Pinheiro, J.C., Bates, D., Debroy, S. & Sarkar, D. (2004). nlme: linear and nonlinear mixed effects models. R package version 3.1-53.
- Press, W.H., Teukolsky, W.T., Vetterling, W.T. & Flannery, B.P. (1992). *Numerical recipes in C: the art of scientific computing*. 2nd edn. Cambridge: Cambridge University Press.
- R Development Core Team. (2004). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for statistical computing. <http://www.R-project.org>.
- Reby, D., Joachim, J., Lauga, J., Lek, S. & Aulagnier, S. (1998). Individuality in the groans of fallow deer (*Dama dama*) bucks. *J. Zool. (Lond.)* **245**, 79–84.
- Reby, D. & McComb, K. (2003a). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Anim. Behav.* **65**, 519–530.
- Reby, D. & McComb, K. (2003b). Vocal communication and reproduction in deer. *Adv. Study Behav.* **33**, 231–264.
- Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W.T. & Clutton-Brock, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proc. Roy. Soc. Lond. Ser. B* **272**, 941–947.
- Riede, T. & Fitch, W.T. (1999). Vocal tract length and acoustics of vocalization in the domestic dog *Canis familiaris*. *J. Exp. Biol.* **202**, 2859–2867.
- Seyfarth, R.M. & Cheney, D.L. (2003). Signalers and receivers in animal communication. *Annu. Rev. Psychol.* **54**, 145–173.
- Sonntag, C.F. (1921). The comparative anatomy of the koala (*Phascolarctus cinereus*) and vulpine phalanger (*Trichosurus vulpecula*). *Proc. Zool. Soc. Lond.* **39**, 547–577.
- Vannoni, E., Torriani, M.V.G. & McElligott, A.G. (2005). Acoustic signalling in cervids: a methodological approach for measuring vocal communication in fallow deer. *Cognition Brain Behav.* **9**, 551–566.
- Venables, W.N. & Ripley, B.D. (2002). *Modern applied statistics with S*. 4th edn. New York: Springer.
- Weissengruber, G.E., Forstenpointner, G., Peters, G., Kübber-Heiss, A. & Fitch, W.T. (2002). Hyoid apparatus and pharynx in the lion (*Panthera leo*), jaguar (*Panthera onca*), tiger (*Panthera tigris*), cheetah (*Acinonyx jubatus*) and domestic cat (*Felis silvestris f. catus*). *J. Anat.* **201**, 195–209.
- Wiley, R.H. & Richards, D.G. (1982). Adaptations for acoustic communication in birds: sound propagation and signal detection. In *Acoustic communication in birds*, 1: 131–181. Kroodsma, D.E. & Miller, E.H. (Eds). New York: Academic Press.
- Yoccoz, N.G., Mysterud, A., Langvatn, R. & Stenseth, N.C. (2002). Age- and density dependent reproductive effort in male red deer. *Proc. Roy. Soc. Lond. Ser. B* **269**, 1523–1528.