Vocal Communication and Reproduction in Deer

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I. Introduction

Despite their reputation for being elusive, deer are in fact highly vocal animals. Conspicuous calls have been systematically found in both sexes of all studied species, and one genus, the barking deer or muntjac, owes its vernacular name to a disposition to vocalize loudly. Males of fallow deer actually have calling rates that are among the highest reported for any terrestrial mammal. Deer vocalizations are also notable for their diversity, ranging from dog-like “alarm” barks to high-pitched, whistle-like mating bugles. In line with other mammals, the typical contexts in which individuals vocalize include social contact (mainly between dominants and subordinates), mother-young interactions, encounters with predators (pursuit deterrent and alarm calls) and, most notably, reproduction (territorial defense, mate attraction and male-male competition).

Reproductive calls of polygynous deer have been of particular interest to behavioral ecologists because red deer roaring provided the first convincing example of vocally mediated male-male assessment in a mammal (Clutton-Brock and Albon, 1979). Since then research has expanded rapidly to examine the wider functions of these sexual calls not only in red deer but also in other deer species. In this review, our aim is to draw together studies that span almost 25 years, and demonstrate how complementary approaches (including anatomical examination and recently developed acoustic analysis and synthesis techniques) can enhance our understanding of the structure, function, and possible evolutionary history of what constitutes an unusually complex array of vocal displays. We also highlight future directions that research might take given recent advances in our understanding of mechanisms of vocal
production in deer and the new technology now available for analyzing the complex structure of mammal calls.

The taxonomy of the deer family is still under debate, but a schematic phylogenetic tree is presented in Figure 1. In our review, we regroup deer species into two broad categories based on the nature of their mating systems. The first group, which we call “solitary deer,” is composed of small, solitary species that usually dwell in forests and are often territorial. Males of these species are monogamous or exhibit mild polygyny, typically without harem defense. This group contains most of the primitive deer: muntjac deer, the Chinese water deer, the roe deer, and most New World Odocoileinae (with the exception of the South American pampas deer *Ozotoceros bezoarticus* and swamp deer *Blastocerus dichotomus* which live in large herds). The moose, despite being the largest living deer, can also

![Schematic phylogenetic tree for the family Cervidae. Deer are thought to have originated in Asia ca. 20 million years ago. The modern deer family (Cervidae) is composed of 44 species, grouped into 4 subfamilies and 17 genera. Two subfamilies, regarded as primitive due to ancestral-like characteristics (small size, externally visible canines, simple spikes or no antlers) are exclusively Asian, namely the Chinese water deer (Hydropotinae), and the muntjacs (Muntiacinae). A third group (Odocoileinae) consists of the Eurasian roe deer (*Capreolus capreolus*), 12 species of New World deer (including the white tailed deer *Odocoileus virginianus*), and two large species with circumpolar distributions, namely the moose (*Alces alces*) and the reindeer (*Rangifer tarandus*). The fourth and essentially Eurasian subfamily, the Cervinae or “true deer,” contains 4 genera and 14 species including père David’s deer (*Elaphurus davidianus*), fallow deer (*Dama dama*), four species of axis deer (*Axis axis, A. porcinus, A. kuhlii, and A. calamianensis*), and the genus *Cervus*, which itself includes sika (*Cervus nippon*), barasingha (*Cervus duvauceli*), Thorold’s deer (*Cervus albirostris*), Eld’s deer (*Cervus eldi*), 3 species of sambar (*Cervus unicolor, C. mariannus, and C. timorensis*), and the red deer (*Cervus elaphus*).
be categorized as solitary, and males form mating pairs with females in most habitats (Geist, 1990). The second group is composed of the large, gregarious, and polygynous species. It contains most of the 14 Eurasian species of Cervinae (including the fallow deer, all red deer subspecies, the chital, the sambar, the barasingha, and the sika deer) and one circumpolar member of the Odocoileinae, the reindeer. Unfortunately, with the exception of the Indian muntjac (Oli and Jacobson, 1995), Reeve’s muntjac (Yahner, 1980), sika deer (Minami and Kawamichi, 1992), and white tailed deer (Richardson et al., 1983; Atkeson et al., 1988), little or no data are available on the vocal behavior of the vast majority of the Asiatic and American deer, as research has instead focused on the more accessible Eurasian species.

II. Reproductive Calls in Solitary Deer

A. Mating Calls

All the small, solitary and forest dwelling deer, which typically exhibit primitive morphological traits, are also distinctive in lacking rut-specific loud-calls. The only references to mating calls in the literature on these species report short-range calls exchanged by males and females during various courting behaviors. In their description of the vocal repertoire of the Indian muntjac (Muntiacus muntjak), Oli and Jacobson (1995) report no call that is exclusively linked to sexual interactions, although a non-specific grooming call is described. In the white tailed deer (Odocoileus virginianus), a “tending” grunt of moderate intensity (Atkeson et al., 1988) is uttered by bucks courting estrous does. Highly aroused roe deer bucks give rasps during the rut, usually while chasing does in estrus, while roe deer does that are chased in turn give squeal-like “unease” calls (Danilkin and Hewison, 1996).

A similar pattern is observed in the much larger, but usually monogamous, moose. Scandinavian moose bulls give a series of muffled grunts when they approach opponents or when they court cows (Reby and Cargnelutti, 1999). This short, low frequency vocalization is relatively soft, suggesting it functions primarily in short-range communication (Geist, 1990; Reby and Cargnelutti, 1999). Moose cows respond to male grunts with a soft, repeated short call (Geist, 1990; Reby and Cargnelutti, 1999) and give longer “appeasement” moans to approaching bulls when they are non-receptive, usually while moving away (Reby and Cargnelutti, 1999). Although hunters mimic appeasement calls to draw in bulls, there is no published evidence to demonstrate that solitary moose cows actually use
these calls to attract males. Moose in open habitat and at high densities have been reported to gather harems (Geist, 1990), and the effect of this plasticity on the vocal behavior would be an interesting theme for future studies.

B. Barking and Territoriality

While no loud “rutting” calls have been unambiguously identified in the monogamous or slightly polygynous solitary deer, all deer give loud, harsh bark-like calls when they detect potential danger (Putman, 1988; Reby et al., 1999a). In solitary species, these calls are largely aimed at informing the predator that it has been detected (white tailed deer: Hirth and McCullough, 1997; Lagory, 1987; muntjacs: Yahner, 1980; Wiles and Weeks, 1981; roe deer: Reby et al., 1999a), but recent studies of barking in roe deer have suggested that this vocalization is also associated with reproductive behavior, specifically in the context of territoriality (Reby et al., 1999a). Roe deer males bark more than females, and do so most during pre-territoriality and territoriality (Reby et al., 1999a). Playback of barks mimicking intrusion by other bucks showed that older bucks are more likely to bark in response to intruders within their territories, and do so particularly when intruders are young males who could pose a threat because of their territory-less status (Reby et al., 1999a). A study of roe deer calls (Reby et al., 1999b) identified strong sex- and age-related differences in acoustic structure: The calls of females and juveniles have more energy concentrated in the upper part of the frequency spectrum than those of adult males, suggesting that such acoustic cues could provide the basis for the differential responses of adults observed in the playback experiments. Reby et al. (1999b) also found that male barks were individually distinctive, potentially enabling bucks to discriminate between their established neighbors and intruding strangers.

III. Reproductive Calls in Gregarious Species

In contrast to solitary deer, gregarious deer compete intensely for females. Intra-sexual competition has resulted in the evolution of obvious sexual dimorphism, with males possessing elaborate weapons (antlers) and sexual displays. Vocal displays are highly developed, with all the males of the gregarious species giving loud repeated calls throughout the period of reproduction (rut). The rutting calls of these species vary widely, for while European red deer roar (Clutton-Brock and Albon, 1979), American red deer (also called wapiti or American elk) bugle (Bowyer and Kitchen,
1987), fallow deer groan, sika deer moan and howl (Minami and Kawamichi, 1992), barasingha yodel (Schaller, 1967; McComb and Reby, personal observation), and reindeer grunt (Lent, 1975; Reby and Cargnelutti, 1999). Although the highly seasonal nature of loud calling clearly indicates that it is directly and exclusively linked to reproductive activity, the precise nature of the information that is broadcasted and the way in which it is encoded in the signal is far from obvious. The great interspecific variability in the rate of calling, the posture that accompanies vocalization, and the acoustic structure of calls, suggests that different kinds of information, intended for a range of receivers, may be broadcast in a variety of ways. Different investigative approaches have produced complementary findings and a larger picture is now starting to emerge. While early studies of the function of reproductive calls in polygynous deer concentrated largely on conspicuous features of signal delivery (primarily calling rate), more recent studies have explored the importance of detailed acoustic cues contained in individual calls and calling bouts.

A. Studies of Call Rate

Calling rate is a dynamic variable that can provide receivers with a range of information over different time-spans. Long-term calling rate is likely to reflect the quality of the caller, as it should be related to the individual’s ability to sustain the physiological costs of maintaining high rates of signal delivery. Short-term variations in call rate may provide a more specific index of the current physical condition of the caller and its level of motivation in relation to the resources being defended and to the threat posed by its current opponent. A number of key studies have focused on linking short- or long-term calling rates to physical and contextual variables including age, body weight, mating success, presence of male competitors and potential mates, and stage of the rut. Here two species have received particular attention, the fallow deer and the red deer, as they are very common in western Europe in free-ranging populations and in parks and farms. Red deer males (stags) give bouts of loud roars when they herd females and during contests with male competitors. Bouts are composed of 1 to 11 roars of variable intonation, quality, and duration (Reby and McComb, 2003). The rate at which males call can be very high, averaging 2 roars per minute throughout the 24 hours in red deer stags during the rut (Clutton-Brock and Albon, 1979) and reaching a maximum of around 8 roars per minute during the roaring contests that precede fights. Fallow deer males (bucks) generally direct their groan-like vocalizations towards females while approaching, herding or chasing them, and towards mature and young males (Braza et al., 1986). The groan is a
short, low-pitched and stereotyped vocalization that is repeated in long series at rates varying between 17 groans per minute (in the absence of females during the pre-rut period) and 54 groans per minute (in presence of females during the rut; McElligott and Hayden, 1999). In fallow deer the most successful males have calling rates that peak at more than 3000 groans per hour (McElligott and Hayden, 1999), suggesting that this is potentially a very costly behavior.

1. Calling Rate and Male-Male Contests

Working on a free-ranging population of red deer on the Island of Rum (Inner Hebrides, Scotland) Clutton-Brock and Albon (1979) identified roaring rate as an assessment cue that determines the outcome of roaring contests between red deer stags. When one red deer stag is challenging another for the possession of a harem, he typically approaches his opponent and the two start to exchange roars directly. After this roaring conversation, the stags may or may not escalate to either a parallel walk, where they parade tensely up and down in parallel (usually roaring as they do so) or to a full-blown fight. Clutton-Brock and Albon (1979) found that fights were more often preceded by roaring contests in which the challenger roared more frequently than his rival than the other way round. Moreover, they found that roaring rates in contests were well correlated with a measure of fighting ability and that average roaring rate probably reflected condition as it varied with stage of the rut (Clutton-Brock and Albon, 1979; McComb, 1988). When Clutton-Brock and Albon (1979) played back roars from a loudspeaker to simulate the presence of a rival stag, stags would increase their roaring rate to match that of the challenger unless the challenger was roaring so fast that they were apparently unable to do so. This provided experimental evidence that stags only continue with a challenge if they can outroar their opponent. As a result of roaring contests, and the further visual and vocal assessment possible in parallel walks, relatively few challenges end in costly fights (Clutton-Brock et al., 1979). They suggested that roaring rate is an honest indicator of fighting ability (and an evolutionarily stable assessment cue) because of the energetic costs associated with maintaining high roaring rates (Clutton-Brock and Albon, 1979).

McElligott and colleagues (McElligott and Hayden, 1999, 2001; McElligott et al., 1998, 1999), have recently conducted a study of mating strategies in fallow deer in Phoenix Park (Dublin, Ireland), including analyses of short- and long-term vocal display rates. These authors found that harem-holding bucks groaned at higher rates in the presence of nearby vocal males and suggested that the signal conveyed by these short-term groaning rates was primarily a threat aimed at rivals (McElligott and
Bucks achieved their highest call rates (averaging 71.6 groans per minute) immediately after copulating, when it is proposed that signallers transmit information to nearby males on their condition and motivational state (McElligott and Hayden, 2001). While these results indicate that differences in calling rate may provide competitors with information on a buck’s motivation and fighting ability, they do not exclude the possibility that high calling rates are simply a by-product of the higher levels of activity that bucks show when rivals are present. Playback experiments comparable to those already conducted on red deer (Clutton-Brock and Albon, 1979) are still required to directly test whether competitors adjust their agonistic behaviour on the basis of short-term variation in groaning rates. However, in line with the hypothesis that the groaning rate acts as a signal between males, immature males decrease their rates of groaning in response to playbacks of groans from mature males, whereas mature males increase their groaning rates in this situation (Komers et al., 1997). Overall, these results suggest that fallow deer bucks vary their groaning rate in relation to the presence and quality of competitors, including the indirect costs of inviting contests with surrounding and potentially stronger males.

2. Effects of Calling on Females

In both fallow and red deer, there is evidence that rutting calls do not function solely to mediate competition between males. In playbacks conducted under controlled conditions on deer farms, red deer females exposed to male roars during the pre-rut period conceived earlier than females who were not, providing evidence that calling can advance ovulation (McComb, 1987). Moreover, red deer roaring appears to influence mate choice decisions. Using a two speaker playback design, McComb (1991) demonstrated that red deer hinds were more likely to look at and move towards the speaker which simulated a stag roaring at a higher rate, even at points in the roaring sequence when both delivered the same number of roars. Hinds also showed a preference for the caller that initiated bouts of roaring. High roaring rates may thus confer advantages in inter-sexual choice as well as intra-sexual competition.

Red deer females also appear to attend to the particular roaring characteristics associated with the stag whose roars they hear most often. Using playback experiments based on the habituation-discrimination paradigm, Reby et al. (2001) found that hinds are able to discriminate between the roars of their current harem holder and those of other neighboring stags (Reby, 1998; Reby et al., 2001), in accordance with previous findings that red deer roars contain sufficient acoustic cues to identify the caller (McComb, 1988; Reby, 1998). Reby and colleagues
suggested that estrous females could benefit by choosing to mate with males that are most familiar to them (i.e., those who are able to spend more time and effort in retaining them within a harem and in roaring at them). Over the course of the breeding period, red deer hinds may progressively become familiar with the vocalizations of the stag in whose harem they spend most time. The degree of familiarity that a given female has with a particular stag’s roars should result from the cumulative extent of her exposure to his roars. A combination of factors is likely to affect this including the duration of exposure, the rate of roaring during exposure and the loudness of the roars (harem holders’ roars will be received at a higher amplitude simply because of proximity).

Studies of long-term groaning rates in fallow deer also indicate that calling rate may influence mate choice and provide some support for the familiarization hypothesis. McElligott et al. (1999) identified a strong correlation between groaning activity and mating success in fallow deer bucks. The bucks who achieved most matings were those who had initiated vocal activity early in the season and who had remained vocal on most days. This led the authors to conclude that females may discriminate between bucks on the basis of long-term investment in vocal activity. Since fallow deer bucks also have individually distinctive vocalizations (Reby et al., 1998), it was proposed that bucks may call early and repeatedly in order to familiarize females with their vocal characteristics (McElligott et al., 1999). In this scenario, the level of familiarity with a male’s rut calls could be a good indirect indicator of his fitness, as it reflects his ability to call at a high rate despite the direct and indirect costs of doing this. However, the familiarization hypothesis has yet to be directly tested in fallow deer, and further studies are required in both fallow and red deer to elucidate how the identity of the caller and his calling rate interact to affect mate choice.

B. STUDIES OF THE ACOUSTIC STRUCTURE OF CALLS

While the studies described above indicate that calling rate clearly constitutes a signal of fitness and motivation during intra-sexual competition and inter-sexual choice, it has become evident that additional information on the phenotypic attributes of the caller is potentially available in the detailed acoustic structure of calls. The acoustic structure of male mating calls in polygynous deer is unusually diverse, with acoustic variation reaching dramatic levels across different species of the Cervinae (Fig. 2) and even across geographic subspecies of Cervus elaphus (Fig. 3). In recent years some progress has been made in understanding the underlying mechanisms that generate this acoustic variability.
Fig. 2. Variation in rutting calls of three species from the subfamily Cervinae. (a) Fallow deer groans: three successive stereotyped vocalizations extracted from a bout (full details in text). (b) Barasingha (*Cervus duvaucelii*) yodels; last 6 notes in the yodel are shown; these vocalizations are unusually long calls composed of 9 to 27 two-toned notes (average 19, n = 67, Schaller, 1967). (c) Sika deer (*Cervus nippon*) moan: one exemplar of the typical call is shown; these calls usually start with a very high pitched whistle followed by a short noisy section exhibiting nonlinear phenomena (visible between 2 and 2.4 sec in this spectrogram), and terminate with a tonal section characterized by a lower fundamental frequency.
Fig. 3. Variation in rutting calls of red deer subspecies. (a) Bugle of American red deer (*Cervus elaphus canadensis*, also called elk or wapiti). This call is a high pitched, strongly modulated whistle. A wide-band noisy component, possibly generated by turbulence in the vocal tract, highlights the formant frequencies, which are well defined despite the high pitched source. (b) Scottish red deer (*Cervus elaphus scoticus*) roar. The pitch of red deer common roars is intermediate, and the fundamental frequency contour is modulated. Formant frequencies are well defined and modulated, the dramatic drop at the beginning of the call reflects the extension of the vocal tract. (c) Corsican deer (*Cervus elaphus corsicanus*) roar. The Corsican deer roar is a tonal, very low pitched call. As in red deer, formant frequencies are very well defined and drop dramatically at the beginning of the roar.
Bio-acoustic approaches have the potential to reveal what information is conveyed in acoustic variability by relating variation in spectral-temporal components of calls to relevant aspects of the physical stature and internal state of callers, or to the social context of calling. The perceptual and functional relevance of these components can then, in theory, be tested on the relevant receivers using playback experiments that present synthesized stimuli in which the acoustic parameters of interest are altered to mimic the variation observed under natural conditions. Used in combination, acoustic analyses and playback of re-synthesized calls provide powerful tools for elucidating the relevance of variation in acoustic parameters.

1. The Source-Filter Theory of Call Production

Recently the ‘‘source-filter’’ theory of human voice production (Fant, 1960) has been generalized to the study of other mammals’ vocalizations, providing a successful causal framework for the exploration of the acoustic structure of most mammal calls (primates: Lieberman et al., 1969; Owren, 1990; Fitch, 1997; cats: Carterette et al., 1979; dogs: Riede and Fitch, 1999; deer: Reby and McComb, 2003; elephants: McComb et al., 2003; see Fitch and Hauser, in press, for a review). This theory states that any mammalian-voiced signal results from a source signal produced in the larynx being subsequently filtered in the cavities of the vocal tract (Figure 4; Fant, 1960). The source signal, or ‘‘glottal wave,’’ is generated inside the larynx by the vibration of the vocal folds. It typically consists of a quasi-periodic signal, the spectrum of which is composed of a series of harmonically-related frequency components known as the fundamental frequency and its overtones. The value of the fundamental frequency is responsible for the pitch of the vocalization, and the way in which it is modulated affects the pitch contour or intonation. This source signal then passes through the supra-laryngeal vocal tract, consisting of the pharynx and the mouth or the nasal cavity, which acts as a filter that selectively amplifies certain frequencies in the source signal before it finally radiates out through the mouth and/or nostrils. The broadband frequency peaks resulting from this filtering process are termed ‘‘formants’’ (Fant, 1960). A well-reasoned and widely-accepted assumption of the applicability of source-filter theory to non-human mammals is that the vibration of the vocal folds and the vocal tract resonances are not coupled and thus can vary independently (Fitch and Hauser, in press).

The source-filter theory is a very productive framework for examining the reproductive vocalizations of deer, because it links acoustical features of the calls with their mechanisms of production. The variation in acoustical features (the fundamental frequency, the formants, etc.) can be related to variation in relevant anatomical characteristics of the caller,
such as its body size or its vocal behavior. For example, the length of the vocal folds, or the length of the vocal tract, which are likely to co-vary with body size, have the potential to affect the values of the fundamental frequency or formant frequencies respectively (Fitch and Hauser, in press). This enables bio-acousticians to investigate which acoustical features of vocal signals can provide receivers with direct information on physical and motivational attributes of the caller—variations in the morphology, size, or control of the vocal apparatus will result in predictable variation in call structure. This integrated approach has so far only been applied to loud calling in European red deer and fallow deer, but research is in progress that will extend it to American wapiti and Corsican deer (Fitch, unpublished data; Cargnelutti, unpublished data).

2. **Functional Anatomy of the Vocal Apparatus in Red and Fallow Deer Males**

An important step in linking the acoustics of a call to its mode of production is to investigate the functional anatomy and sound production behavior of the caller. In the case of red deer and fallow deer males,
careful observation of the throat region while rutting calls are being produced reveals the consistent movement of a large ventral protuberance up and down the neck (Whitehead, 1993). Dissections and radiography by Fitch and Reby (2001) have confirmed that this protuberance is the underlying larynx. Radiographic investigations have identified an unusually low resting position (relative to the skull base) for the larynx in both red and fallow male deer, but not in females of these species, nor in the roe or white-tailed deer specimens of both sexes that were dissected by the authors (Fitch and Reby, 2001). The retraction of the larynx in the males of these species is based on two anatomical innovations (Fig. 5). First, the connection of the larynx with the hyoid cartilage and the skull is elastic. In herbivores, this connection is typically made by a short and tough thyro-hyoid membrane, which limits downward laryngeal movement relative to the hyoid and tongue. However, in red and fallow deer males

Fig. 5. Anatomy of the vocal apparatus in a fallow deer male. This radiograph of the head and neck of a fallow deer buck shows the low position of the larynx, the absence of direct articulation between the thyroid and the hyoid cartilages, and the elongated velum [from Fitch and Reby, 2001].
the connective tissue linking the larynx to the hyoid apparatus is composed of a highly elastic thyro-hyoid membrane and a loose elongated thyro-hyoid muscle, enabling the larynx to be mobile. Second, the males of red and fallow deer need particularly strong muscles to extend their vocal tract up to several thousand times per hour, as they do during the three to four weeks of vocal activity. The sterno-thyroid and sterno-hyoid muscles, which pull the larynx towards the sternum, are highly sexually dimorphic. These muscles are powerfully developed in males and increase in size prior to the rut (Fitch and Reby, 2001; Lincoln, 1971). Examination of video recordings of red deer stags shows that the larynx is pulled as far down as the sternum during a majority of roars (Fitch and Reby, 2001). In fallow deer, the larynx is pulled only halfway between its resting position and the sternum (Reby, personal observation). In both species, the pharyngeal cavity that results from this descended larynx is partitioned by an elongated and elastic soft palate which stays in contact with the epiglottis in the resting position (Fitch and Reby, 2001).

3. Acoustic Characteristics of Red and Fallow Deer Rutting Calls

Having examined the functional anatomy of the vocal apparatuses of red and fallow deer males, the next step is to examine the acoustic structure of rut calls given by these species, in order to relate the functional anatomy of the callers to the acoustic structure of their vocalizations.

a. Red deer rut calls

The vocal repertoire of red deer stags during the rut consists of five distinct vocalizations, which can be classified with reference to their acoustic structure, the behavior of the caller and the context of calling (Reby, 1998). The first of these, known as common roars (Figure 6a) are given in bouts during both male-male contests and active herding of females. The acoustic structure of the common roar reflects changes in vocal fold vibration and vocal tract shape that occur during sound production (McComb, 1988; Reby, 1998; Fitch and Reby, 2001). Common roars typically sound tonal and have a spectral structure that shows well-defined harmonics. However, noisy segments, characterized by non-linear phenomena, are often observed during the course of vocalizations (see Section IV.B.).

The fundamental frequency in common roars generally ranges between 65 and 140 Hz (average 112 Hz, Reby and McComb, 2003), although some roars given at the end of a bout by less active animals can have an unusually low F0 (down to 36 Hz) which gives the call a pulsed sonority. The fundamental frequency contour typically rises at the beginning of the call and falls suddenly at the end, reflecting variation in the rate of vibration of the vocal folds that occurs in the larynx as a result of varying
vocal fold tension and sub-glottal pressure during vocalizing. It can be strongly modulated, with an average of 1.9 inflection points per second and a frequency variation of 72 Hz per second (Reby and McComb, 2003).

As expected from the source-filter theory, the formant frequencies in red deer roars vary independently from the fundamental frequency. Immediately before vocalizing, and during the first part of the roar, the stag lowers its larynx and stretches its neck by raising its head, which increases the length of its vocal tract. The immediate consequence of this behavior is a dramatic decrease in formant frequencies which, in spectrograms, are seen to move towards a lower plateau (Figure 7) that corresponds to the maximum extension of the vocal tract in the roar (Fitch and Reby, 2001). The stag then generally keeps its vocal tract fully extended, so that formant frequencies remain unchanged for the main
Fig. 7. Top. Retraction of the larynx (indicated in the photograph by white arrow) during roaring in red deer leads to a sharp decrease in formant frequencies. Middle. Spectrogram of the emitted roar, showing decreasing formant frequencies (F1–F6) during calling (note that the narrower, evenly spaced and rising frequency components in the first half of the roar represent the harmonics). Bottom. Illustration of the extension of the vocal tract that accompanies the lowering of the larynx towards the sternum [adapted from Fitch and Reby, 2001].
section of the call. In the final part of the roar, formants rise as the larynx and head come back to their initial resting positions. Sometimes the stag relaxes its neck before it relaxes its larynx, which causes a partial rise of the formant frequencies. In the course of a roaring bout, the stag does not completely shut its mouth between two consecutive roars and its head does not fully return to the horizontal position, so that the fall and rise of the formant frequencies in roars that are given in the middle of the bout are usually less marked (Fig. 6a).

Some roaring bouts include louder vocalisations known as “harsh roars” (Fig. 6b). The acoustic structure of harsh roars is similar to that of the noisiest segments of the more typical “common” roars, with the fundamental frequency and harmonics poorly defined or absent. Harsh roars are characterised by weaker formant modulation and the absence of a pronounced drop in formant frequencies at the beginning of the roar, reflecting the static body posture adopted by the animal during the production of this call. In harsh roars the stag fully extends its neck (the head is raised so that the lower jaw is aligned with the lower part of the neck) and lowers its larynx down to the sternal limit before vocalising. Harsh roars tend to occur in situations of intense activity, after a roaring contest or during a period of repeated herding. Bouts delivered in these situations often start with a series of short “grunt roars” followed by one or more harsh roars. While these shorter vocalisations are acoustically very similar to harsh roars, they may have a distinct function as their abrupt staccato quality renders the caller particularly conspicuous. It is possible that they serve to focus the attention of receivers on the harsh roars that follow—the latter being particularly adapted for advertising the caller’s body size to a maximum (see Section III.B.5.b).

The final two call types are barks. Series of short, explosive “chase barks” (6c) are typically given by stags as they chase a hind, a young competitor, or a defeated opponent (Clutton-Brock et al., 1982; Reby, 1998). This call seems homologous to the belches of fallow deer bucks described below, and to the aggressive snorts given by males of sika deer during chases (Minami and Kawamichi, 1992). Longer loud “barks” (6d) are also given by stags as they stand motionless and may be delivered on their own or immediately before a bout of common roars. Barking in polygynous deer is a relatively common alarm call, usually given by females surrounded by matrilineal kin (red deer: Long et al., 1998; fallow deer: Álvarez et al., 1975; sika deer: Long et al., 1998; sambar: Schaller, 1967; chital; Schaller, 1967). However, when red deer stags bark, they typically do so towards females during intense herding in situations where no potential danger occurs. Anecdotal observations suggest that barking by red deer stags during the rut may constitute a manipulative use of the
alarm call -functioning to encourage defensive bunching by the hinds and thus to increase the cohesion of the stag’s harem (Reby and McComb, personal observation).

A study of individual characteristics in red deer roars using “cepstral” analysis and Hidden Markov Models for modeling individuality in the dynamics of the spectral envelope (formants) has shown the existence of consistent acoustic differences between the roars of different stags (Reby, 1998). The models trained using the common roars from seven individuals could also correctly recognize the identity of the caller when they were used to classify other types of calls from the same animals (harsh roars, chase barks, and barks). This suggests that some cues to identity conveyed by the formant frequencies are shared in these four call-types. Such across-call cues to identity in acoustic structure, which constitute the equivalent of the individual “voice” of human speakers, have so far been identified in only one other species of non-human mammal, the rhesus monkey (Macaca mulatta, Rendall et al., 1998).

b. Fallow deer rut calls  As previously described, the most common rut vocalizations given by fallow deer bucks are long series of stereotypical groans. The groan is a short, low-pitched, and stereotyped vocalization that sounds guttural (Fig. 8a). Because of their unusually low fundamental frequencies (ranging between 21 and 71 Hz; Reby et al., 1998), groans are
perceived as “pulsed” by human listeners. The fundamental frequency or pulse rate is highly variable within one individual, and appears to be related to the level of activity of the recorded animal (Reby et al., 1998). Moreover in some bucks, groans become noisy in the late rut (Reby et al., 1998), a likely consequence of vocal fatigue, and very active bucks appear to give a softer groan during the inhalation between each successive full-throated groan. In addition to their main groaning vocalization, when they chase other males, fallow deer bucks also give “belches,” distinctive and guttural calls which consist of a series of widely spaced single pulses (Figure 8b; Reby and Cargnelutti, 1999).

Spectrograms of fallow deer groans show well-defined and unevenly-spaced formants. The extension of the vocal tract, which is achieved by raising the head and lowering the larynx toward the sternum during each groan, results in a consistent drop in formant frequencies during the first part of the groan (Figure 8a). The formant patterns of different fallow deer bucks are individually distinctive—a neural network classification using spectral variables to model the formants allowed the caller of a groan to be identified in 88% of cases (Reby et al., 1998). Further studies of fallow deer rutting vocalizations are now needed to investigate relationships between acoustic variables (particularly fundamental frequency and formant frequencies) and physical and motivational characteristics (particularly size, age, mating success, and context of utterance), in line with analyses that have recently been conducted on red deer stags.

4. Quantitative Studies of Source Characteristics in Red Deer Roars

In mammals generally, investigations of how information on callers’ attributes are coded in vocalizations have mainly focused on the potential for source-related fundamental frequency to provide an accurate cue to body size (Hauser, 1993; Masataka, 1994). Such an emphasis has arisen from the assumption that the length of the vocal folds should increase with body size and constrain fundamental frequency range (Titze, 1994). On this basis it has often been predicted that larger animals should produce lower pitched vocalizations (Morton, 1977). However, the assumption that vocal fold length should correlate with body size had not, until recently, been tested in any non-human mammal. Both anatomical and acoustical measurements have now been performed in red deer (Reby and McComb, 2003; Fitch et al., unpublished).

4.1. Anatomical analyses: vocal fold length, age and body weight

Anatomical analyses were conducted on culled red deer stags (aged 1–14 years) on the Island of Rum to investigate how vocal fold length varies with age and body weight. This work revealed that the length of the vocal folds is positively
correlated with body weight ($r = 0.795$, $p = .0001$, $N = 42$). However, when age is adjusted using multiple regression, the correlation between vocal fold length and body weight disappears ($r = 0.94$, $p = .94$, $N = 42$) and age is revealed to be the main determinant of vocal fold length ($r = 0.7$, $p = .0001$, $N = 42$). In particular, vocal fold length continues to grow throughout the stag’s life, with very old animals having the longest vocal folds, even though stags normally stop growing after they reach six years of age (Clutton-Brock and Albon, 1989). These results suggest that fundamental frequency should decrease with age in red deer stags, but is unlikely to be a good indicator of body weight variation within age categories.

b. Acoustic analyses: fundamental frequency, age and body weight

Acoustical analyses of the common roars of Rum stags (Reby and McComb, 2003) revealed no clear correlations between stag body size, age, or reproductive success and fundamental frequency variables (Reby and McComb, 2003; see also McComb, 1988, 1991). The fundamental frequency is on average higher in sub-adult stags (125 Hz) than it is in adults (107 Hz), as would be expected from the increase in vocal fold length in stags across their lifetime reported above. A similar age-related decrease has been reported between the sub-adult and adult stages in the moans of sika deer (Minami and Kawamichi, 1992). However, fundamental frequency in red deer roars remains highly variable among adults (Reby and McComb, 2003). Moreover, this variation is independent of body weight, as would be expected from the lack of correlation between vocal fold length and body weight.

There are good theoretical reasons for suspecting more generally that F0 range may actually be a poor guide to body size in red deer and other loud calling mammals. Fundamental frequency results from complex interaction between the tissue density, the longitudinal stress and the length of the vibrating portion of the vocal folds (Titze, 1994), a range of factors that may not be constant across individuals. Moreover, more successful stags may achieve higher subglottal pressures and increase the stiffness of their vocal folds as a result of their higher level of activity, two actions that would result in increasing the fundamental frequency in their roars. The high variability in fundamental frequency observed in adult stags may thus result from conflicting factors—F0 may decrease with vocal cord length, but increase with factors such as sub-glottal pressure, which is likely to be higher in stronger animals with higher reproductive success (Reby and McComb, 2003).

In summary, it appears that fundamental frequency variables have limited potential to provide receivers with information on body size. Experiments to investigate the response of male receivers to callers with different
fundamental frequencies have yet to be conducted. However, in a two-speaker playback experiment in which female red deer were presented with the choice between roars with high and low fundamental frequencies, they exhibited no preference for low-pitched roars (McComb, 1991).

c. **Interspecific variation in fundamental frequency**  Looking across polygynous deer within the subfamily Cervinae, there is an apparent lack of correlation between the body size of a species (or sub-species) and the fundamental frequency of its sexual calls (Fig. 2 and 3). For example, although fallow deer are significantly smaller than red deer, the fundamental frequency of fallow deer groans is much lower than that of red deer roars (Fallow deer: 34 Hz, Reby *et al*., 1998; red deer: 112 Hz; Reby and McComb, 2003). Furthermore, within *Cervus elaphus*, the roar of one of the smallest subspecies, the Corsican red deer (*Cervus elaphus corsicanus*) has the lowest fundamental frequency (34 Hz, Cargnelutti and Reby, unpublished data), whereas the whistled bugle of the largest subspecies, the American red deer or wapiti (*Cervus elaphus canadensis*), has the highest (around 1 kHz, despite a body weight that is on average 2.5 times larger than that of western Europe red deer). Variations of this magnitude may reflect a lack of correlation between body size and larynx size across species or even specializations of the shape and histology of the vocal folds. A comparative study of the histology and biometry of the vocal folds across deer species is therefore clearly needed in order to understand the mechanical basis of this counterintuitive variability.

To the human listener, the low-pitched calls of fallow deer and Corsican red deer are barely audible beyond a few hundred meters, in contrast with the higher-pitched red deer roars, wapiti bugles, or sika deer howls, which remain audible over distances of more than a kilometer (Reby and McComb, personal observation). A possible explanation for the variation in the acoustic structure of loud calls described above is that differential selection pressures have adapted call structure in relation to ecological variables, in particular optimal localizability and propagation distance that derive from each species’ habitat, mating system, or mating opportunities. However, the lack of concrete information on the acoustic properties of the habitats in which these species evolved means that it is currently not possible to conduct a meaningful analyses of this sort. Irrespective of the ultimate origins of the extreme variability found in rutting calls of the Cervidae, fundamental frequency range appears to provide little or no indication of body size across and within species.

d. **Heritability of F0 characteristics in red deer stags**  Although red deer and sika deer are two distinct species, they hybridize readily in both
captive and free-ranging conditions to produce hybrids that are also fertile (Harrington, 1973; Putman and Hunt, 1993). Since sika and red deer males have very different calls, the structure of the rutting call produced by hybrid males is of some interest. Long et al. (1998) found that hybrids produced calls with fundamental frequencies intermediate between that of the parent species, providing a broad indication that the structure of the rutting call has a genetic basis. Fundamental frequency may also have a strong heritable component within species. Indeed, preliminary results of a study examining roar fundamental frequency in adult red deer stags and their four to six year old sons indicate that sons inherit the value of the fundamental frequency of their father, in particular the average F0 and the maximum F0 (McComb and Reby, in preparation).

5. Quantitative Studies of Filter Characteristics in Red Deer Roars

Studies that have assessed what information may be conveyed to receivers in the filter-related formants of mammal vocalizations suggest that formants could provide a more reliable indication of body size than the fundamental frequency variables (rhesus monkeys: Fitch, 1997; dogs: Riede and Fitch, 1999). This is a direct consequence of the inverse relationship between formant frequencies and the length of the vocal tract—formant frequencies and average spacing of formant frequencies decrease when the length of the vocal tract increases (Fant, 1960; Titze, 1994; Fitch, 1997). In most mammals, the larynx is tightly attached to the base of the skull, constraining the length of the vocal tract, which correlates strongly with skull size (Fitch, 1997; Fitch, 2000; Fitch and Hauser, in press). Because of this, formant frequencies have the potential to accurately reflect variation in body size. The unusual descended and highly-mobile larynx of red deer males raises the possibility that the average spacing of formant frequencies in red deer roars might not be a reliable, “honest” indicator of body size, since individual stags can actively modify their vocal tract length. However, red deer stags often pull their larynx fully down to the sternum, an anatomical limit beyond which no further retraction is possible (Fitch and Reby, 2001). This upper limit on vocal tract extension may constrain the lowest frequencies of the formants and consequently their minimum spacing in the roar. If this is the case, the lowest frequency of each individual formant and the minimum frequency spacing of the formants, by reflecting the maximum extension of the vocal tract achieved during roaring, may still provide listeners with honest information.

a. Anatomical analyses: vocal tract length, age, and body weight  In order to test whether the length of the vocal tract is positively correlated with the
body weight of the animal, we examined the dimensions of the vocal apparatus in the same sample of culled red deer stags that provided vocal fold measurements (Section III.B.4.a.). We found that the maximum possible vocal tract length (measured as the distance between the sternal attachment of the sterno-thyroid muscle and the incisors) is positively correlated with (carcass) body weight ($r = 0.735, p = .0001, N = 38$), and with age ($r = 0.681, p = .0001, N = 38$). When entered in a multiple regression, weight was identified as the best predictor of vocal tract length ($r = 0.585, p = .0157, N = 38$) and age was no longer significant ($r = 0.173, p = .457, N = 38$). These results strengthen the hypothesis that the frequency spacing of formants achieved when the vocal tract is fully extended should provide an indication of body size in red deer roars.

b. Acoustical analyses: formant frequencies, age, and body weight  Acoustical analyses of the roars of red deer stags in the Rum study population demonstrated that the minimum frequencies and the minimum spacing of the formants in the first roar of each bout provide reliable cues to stag body size and reproductive success (Reby and McComb, 2003). Formant frequencies also decreased with age. Although the latter relationship is probably a direct consequence of the lengthening of the neck and vocal tract that occurs with body growth, it may also result from an increase in the elasticity of the thyro-hyoid ligaments. If the elasticity of these ligaments increases with age, adults could be more efficient than sub-adults at fully extending their vocal tracts and lowering the larynx closer to the sternum. The acoustical analyses demonstrated that within adults, formant frequencies are strongly negatively correlated with body weight, which is in line with the anatomical investigations showing that that animals with heavier pre-rut body weights have longer vocal tracts. The same pattern of relationships was also found between formant frequencies, formant spacing, and an index of reproductive success, which was also closely related to body weight (Reby and McComb, 2003). The minimum spacing of the formants, achieved when the vocal tract is most fully extended, therefore provides an honest indication of body size in red deer roars. This honest advertisement is the result of the morphological constraint imposed by the head and neck length and may be independent of any production cost.

On the basis of the above results, female red deer might be expected to prefer stags whose roars have formants with lower minimum frequencies, as these individuals are likely to be larger and have higher fitness. Furthermore, we would expect males to use formants’ frequencies as an indicator of an opponent’s fighting ability during roaring contests and parallel walks, thereby avoiding fights with older (more experienced) and
larger stags. Adult harem holders, which are less likely to reply to playbacks of young stags’ roars (Clutton-Brock and Albon, 1979) may use filter-related cues to age to identify sub-adult individuals. We are currently testing these hypotheses by playing back re-synthesized roars with modified formants (mimicking stags with various vocal tract lengths) to male and female receivers (Reby et al., in preparation).

c. Evolutionary paths toward laryngeal descent Fitch and Reby (2001) suggested that the descended position of the larynx in red and fallow deer males may result from sexual selection pressures favoring individuals capable of exaggerating the impression of size conveyed by their vocalizations. Individuals with lower than average larynges yielding lower formants would have an advantage in intrasexual competition and mate choice (Fitch and Reby, 2001). However, the evolutionary process responsible for maintaining honesty during the transition from a typical fixed mammalian larynx located high in the neck to a low and mobile one (limited in its position of maximum descent by the sternum) remains unclear. One potential means for maintaining some degree of honesty during this transition is through the persistence, over evolutionary time, of a correlation between the size of the animal and the length of its fully extended vocal tract. This could occur if, for example, animals with stronger sternothyroid muscles were able to stretch their ligaments more efficiently, giving them longer vocal tracts for the same level of ligament elasticity. Such a correlation would have kept the pressure high on receivers to use formants as an indicator of body size, favoring individuals with more extensible vocal tracts (achieved via changes in ligament elasticity, sterno-muscular development or both).

It is possible that during the evolutionary history of red deer there may have been selection for hiding the initial part of the roar where formants convey information about the non-extended vocal tract length. Time-synchronized video analyses of red deer roaring show that most stages start vocalizing when the larynx is 37% of its way down toward the sternum (Fitch and Reby, 2001), completing the descent of the larynx in the middle of the roar and letting it rise again towards the end. Furthermore, our recordings indicate that some stags attenuate the amplitude of the first part of the roar when formant frequencies have not yet reached their lower limit by keeping this part nasalized (Figure 9). Moreover, in harsh roars the larynx is almost always pulled to its lower limit, and the neck fully extended, before the vocalization is given.

d. Descended and mobile larynges in other mammal species The presence of a descended larynx and the ability to vary vocal tract resonances has been
identified on the basis of acoustical and behavioral evidence in fallow deer, European red deer and wapiti (Fitch and Reby, 2001), and in Corsican red deer (Cargnelutti and Reby, in preparation). Males of these species (which represent all the polygynous deer for which the relevant information is currently available) are therefore able to dramatically modulate the average spacing of their formant frequencies by altering the length of their vocal tract. In contrast, females of gregarious deer species and both sexes of solitary deer seem to lack this capability (Fitch and Reby, 2001). More generally, this ability has not been unambiguously demonstrated in any other mammal species, for although big cats are known to have potentially mobile larynges (Hast, 1989; Weissengrüber et al., 2002), the effect of this on the acoustic structure of calls has not yet been studied in detail.

e. Vocal tract length versus vocal tract shape modulation  While the ratio of the length of the pharynx to the length of the oral cavity automatically
increases as the larynx is lowered during roaring and groaning, there is so far no evidence that deer actively modify the shape of their vocal tract in order to generate strong modulations in the relative positions of formant frequencies. In this, they remain identical to other non-human mammals, which also lack sophisticated control of vocal tract shape, and are only capable of limited formant modulation, achieving this by using the lips and lower jaw to alter the shape and the opening condition of the mouth cavity (Lieberman et al., 1969; Hauser et al., 1993; Shipley et al., 1991). Sophisticated modulation of the shape of the vocal tract therefore remains a unique feature of human voice production. The great variety of complex sounds that compose speech are typically achieved by altering the shape of the laryngeal and oral cavities using horizontal and vertical movements of the tongue (Fant, 1960). According to Lieberman and Crelin (1971), the acquisition in human evolution of a low larynx position (unique to humans among the primates), is a necessary condition for having a vocalic space sufficiently large to achieve the acoustic contrasts that are necessary for speech. Interestingly, the descended position of larynges in humans and males of polygynous deer may be analogous, constituting a case of convergent evolution (Fitch and Reby, 2001). At puberty, human adolescent males acquire a slightly longer vocal tract caused by a further descent of the larynx completing the initial descent that occurs in infants and is common to both sexes (Ohala, 1983; Fitch and Giedd, 1999). This extension of the vocal tract (which is concomitant with the sexually dimorphic development of a beard and the elongation of the vocal folds) does not improve the phonetic ability of the adolescent male, but results in speech that has lower formant frequencies (Fant, 1975). The latter observation strongly supports the hypothesis that the descent of the larynx in humans may have initially resulted from sexual selection favoring individuals capable of exaggerating the expression of body size conveyed by formant frequencies in their vocalizations (Fitch and Reby, 2001).

IV. RESEARCH IN PROGRESS AND FUTURE DIRECTIONS

A. FORMANT MODULATION AS A POTENTIAL INDICATOR OF MOTIVATIONAL STATE

Most research on the information contained in the formant patterns of mammal vocalizations has focused on formant spacing as a static cue to body size. However, the mobility of the larynx means that formants in red deer roars are strongly dynamic features (Fitch and Reby, 2001) and the way in which formant frequencies are modulated may provide receivers
with additional information. For a particular caller, the upper and lower limits of each formant frequency are constrained by the minimum and maximum vocal tract lengths achieved. More specifically, the length of the resting, non-extended vocal tract imposes the highest frequency value of each formant, while the length of the fully extended vocal tract sets the lowest frequency value. The modulation of formant frequencies between these two extremes, however, is not constrained. Preliminary observations (Reby and McComb, unpublished) suggest that the dynamics of vocal tract extension differ within stags, and appear related to the level of motivation of the caller. As illustrated in Figure 10, the slope of formants at the beginning of roars and the stability of the plateau when formants have reached their lowest values can vary between roars in a bout. Similarly,

**Fig. 10.** “Lazy” bout of red deer common roars, showing the increase in formant frequencies and the decrease in fundamental frequency that occur between roars across the bout. The minimum average frequency spacing between formants that is achieved during the roar (MinΔF) increases from 238 Hz in the first roar to 340 Hz in the last roar, reflecting a decrease in estimated maximum vocal tract length from 73.5 cm (fully extended vocal tract) to 51.5 cm (rest vocal tract). maxF0 falls independently from 143 to 60 Hz. [See Reby and McComb (in press) for details of the methods used for extracting F0, formant frequencies, formant spacing, and estimated vocal tract lengths.] This can be compared with an active bout from the same stag (shown in Figure 7), where formant frequencies are less modulated and remain close to the minimum plateau (except in the final roar).
stags fail to fully extend their vocal tracts in the final roars of some bouts (Fig. 10). We hypothesize that these dynamic features of formant frequencies may broadcast information about the caller’s experience (maturity) and its current condition or motivational state. The reliability and function of such information, which could be of particular importance as an assessment cue in roaring contests, is currently under investigation.

We already have some indication that red deer stags put more effort into extending their vocal tracts during two contexts of high excitement. First, measurements of formant spacing indicate that when delivering harsh roars, stags extend their vocal tracts by a couple of centimetres more than they do when giving common roars (Reby and McComb, 2003). This additional extension probably arises from stags systematically raising their head to the maximum extent during harsh roaring, thereby fully stretching their necks. It may also reflect a particularly strong muscular effort to bring the larynx closer to the sternum. Analogous behaviors such as lip rounding and protruding, which also marginally increase the length of the vocal tract and lower formant frequencies, have been reported in other mammal species vocalizing during aggressive interactions (Ohala, 1983; Fitch, 1994) and may serve a similar function of signaling high levels of motivation through acoustic size-symbolism. Second, a study of the formant frequencies in common roars given immediately after herding estrous hinds (in comparison with those given outside of this context) has shown that formants in these vocalizations are on average lower (Reby and McComb, in preparation). Preliminary observations of video-footage of herding events suggest that a stag performs the extra vocal tract length extension by raising its head to more fully extend the neck.

B. NON-LINEAR PHENOMENA IN RED DEER ROARS

Another feature of loud calling which may provide receivers with information on male quality and motivation is the periodical quality of individual roars. The potential importance and adaptive significance of non-linear dynamics in mammal vocalizations have only recently been identified and discussed (Wilden et al., 1998; Fitch et al., 2002). Features such as subharmonics and deterministic chaos, reflecting non-linear dynamics in vocal fold vibration during vocal production, are very common in red deer roars. In common roars, subharmonics (visible in spectrograms as harmonically related frequency bands between overtones of the fundamental frequency; Fig. 11) often precede deterministic chaos which is manifested as broadband noise superimposed on the harmonic structure (Figure 11). Moreover, deterministic chaos is an intrinsic feature of harsh roars. Broadband noise in calls of this sort may be ideal for
emphasizing the vocal tract transfer function, highlighting the formant frequencies and providing clear information on body size (Fitch et al., 2002). It is also possible that the occurrence of deterministic chaos during noisy sections of common roars and during harsh roars reflects the caller’s motivational state, as this feature is often associated with very high subglottal pressures. Systematic quantification of these acoustic phenomena should now be carried out in order to relate their occurrence to the quality and motivational state of the signaler and provide the basis for playback experiments to assess their perceptual and functional relevance.

C. THE COSTS OF CALLING

1. Physiological Costs

Although roaring in red deer and the production of analogous calls in other deer species is widely cited as being costly, an important issue raised by Clutton-Brock and Albon (1979) remains: The actual physiological cost of producing these calls has never been quantified. While sexual calling in amphibians is known to involve significant energetic costs (Ryan, 1988),

![Nonlinear phenomena in red deer roars. The arrows point out several of the subharmonics in this roar, which result from period doubling. The black bar indicates a segment of deterministic chaos.](image-url)
the costs associated with call production in warm-blooded vertebrates can be negligible (Horn et al., 1995; Speakman et al., 1989; Russell et al., 1998). Recent advances in our understanding of vocal production in polygynous deer suggest that in these species the actions associated with the extension of the vocal tract (in particular lowering the larynx and raising the head) may constitute an unusual and significant source of energy expenditure that could impose an upper limit on calling rate. A strong positive correlation between the body weight and weight of the sternothyroid muscles in red deer ($r = 0.65$, $p = .002$, $N = 27$, correcting for age) indicates that stronger, heavier males should be able to extend their vocal tract more efficiently. This observation may be at the basis of correlations between roaring rate, fighting ability, and mating success (Clutton-Brock and Albon, 1979; McComb, 1988). However, technology capable of estimating the costs of vocal production in large mammals is required to test this.

2. Indirect Costs

Individuals that produce rutting calls may also incur indirect costs, as the act of calling would be expected to render callers more conspicuous to predators and rivals and may also prevent them from carrying out other important activities. Support for this hypothesis comes from observations that young and injured animals faced with rivals reduce calling rates or suppress signalling altogether (McComb and Reby, 2003; Komers, 1997). Experiments to specifically investigate how animals adjust calling in relation to the presence of rivals or predators are warranted.

V. Summary

The study of vocal communication and reproduction in deer has revealed that males produce an unusually diverse array of rutting vocalizations, with extreme variation occurring both between and within species. Moreover, many of the polygynous deer produce acoustically complex calls in the context of reproduction, in which vocal tract resonances or formant frequencies vary widely over the course of the vocalization. The functional significance of these calls is starting to become clear in the few species where integrated studies have combined observations of calling behavior with anatomical and acoustical analyses, and where playbacks experiments have confirmed the relevance of particular acoustic cues. While this powerful approach needs to be extended to the full range of deer species, it is already obvious that one important factor underlying the acoustic variation is the possession by
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polygynous some male deer of a descended and highly mobile larynx. This anatomical innovation allows them to modulate formant frequencies to an extent that was hitherto unknown in mammals other than humans. In deer this ability appears to have arisen through sexual selection—males lower their larynges to display their vocal tract length and thus their body size to a maximal extent—suggesting that similar selection pressures may have influenced the descent of the larynx in humans. Thus, 25 years of study in this field have led not only to a deeper understanding of the sexually selected cues present in the reproductive calls of deer, but also to important insights into mammalian communication, including the origins of anatomical modifications that may ultimately have enabled human speech production.

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