

Comparison of vocalisations of introduced European red deer stags (*Cervus elaphus*) in north-western Patagonia (Argentina) with native European populations

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Abstract. Polygynous deer are very vocal species, producing calls in various contexts. Male rutting calls in red deer (*Cervus elaphus*) have been most studied in captive and/or free-ranging European populations. The recent application of ‘source-filter theory’ has identified the independent roles of fundamental frequency (F0) and formants in the production of deer calls and demonstrated the relation between formant spacing and anatomical characteristics such as body size. The present paper describes and characterises the acoustical properties of male rutting vocalisations for a free-ranging red deer population located in the ecotone of the eastern Andean cordillera within the Nahuel Huapi National Reserve (Neuquén, Argentina), and is the first acoustic study of free-ranging red deer stags outside their historic distribution. Recordings were made of seven identified and several unidentified stags at the peak of the rut in 2007. Calculated F0 was found to be higher for these identified stags than for Scottish red deer on the island of Rhum. The analysis of formant spacing was used to calculate the length of the vocal tract (VTL) for the seven males studied; values were comparable to those found in stags from Rhum. The longest calculated VTLs within these males corresponded to those of the four stags with the largest antler racks and the only stags holding harems. Previous studies have shown that VTL correlates with body size, age and reproductive success and that these deer have the ability to lower their larynx and extend their vocal tracts to a maximum, which is probably under sexual selection. Our data fit with this explanation. The higher F0s recorded in this population may result from the influence of wapiti genes, known to be present in these deer, because wapiti have a much higher-frequency rutting call, namely, the bugle. Alternatively, they may be related to the mating strategy, which differs substantially from the northern European populations.

Additional keywords: formants, intra-specific variation, mating behaviour, pitch, roars, wapiti.

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Introduction

Communication plays a crucial role in social interactions in deer, as in other group-living mammals. Although not obvious to the casual observer, polygynous deer are very vocal species. Moreover, their vocalisations are notable for their diversity. Calls have been registered in both sexes and in different contexts, such as social contact, mother–young interactions, and male rutting calls, which function in both male–male competition and female choice (Taylor and Reby 2010; Reby *et al.* 2010, 2005; Reby and McComb 2003b). The vocalisations emitted during mating activities have received the most attention, particularly in red deer (*Cervus elaphus*), with captive and/or free-ranging populations having been studied in Scotland, France and Italy (Faravetto *et al.* 2006, McComb 1987, 1991; Pépin *et al.* 2001; Reby and McComb 2003a, 2003b; Reby *et al.* 2001, 2005, 2010; Fitch and Reby 2001).

The ‘source-filter theory’ of mammalian sound production hypothesises that the vocalisations produced result from two independent processes. First, the sound is generated by the vocal folds of the glottis, which produce the F0. The sound then passes through the cavities of the superior vocal tract where it is filtered by the resonant frequencies of the cavities. Some frequencies are augmented (the formants) and others are dampened (Taylor and Reby 2010). The distribution of the formants or formant frequency dispersion (ΔF), unlike F0, is related to the variation in the anatomical characteristics of the caller, such as body size, because it accurately reflects the VTL (Fitch 1997; Reby and McComb 2003a, 2003b). Using source-filter theory, the different contributions of the source, as F0, and the filter, as ΔF , have clarified the form of production of many animal calls, how variations in F0 can reflect hormonal or motivational changes and how ΔF is an accurate reflection of

the VTL and, thus, of body size (Taylor and Reby 2010). In red deer and fallow deer (*Dama dama*), the use of this theory led to the discovery that stags of these species can lower their larynges during vocalisation, thereby increasing their VTLs, decreasing the ΔF , and increasing their apparent size (Reby and McComb 2003a; McElligott *et al.* 2006). In red deer, ΔF is used by stags to evaluate their opponents and by hinds to select a mate (Reby *et al.* 2005; Charlton *et al.* 2007).

Here, we present the first study of vocalisations of free-ranging red deer stags outside their historic distribution. Exotic red deer were first introduced to Argentina in the period 1902–1910 by Pedro Luro to the La Pampa Province. The records from the company importing the red deer showed them all to be of Austrian–Hungarian stock from the mountains of the Alps and Karpaten (Wollenhaupt 1983). In the early 1920s, Robert Hohmann brought 20 individuals from Parque Luro to the ‘estancia’ Colluncó near San Martín de los Andes, from where they were liberated in 1922. In 1924, individuals from Colluncó were translocated to an enclosure on Peninsula Huemul in Nahuel Huapi National Park, to be later released in 1926 (reviewed in Flueck and Smith-Flueck 1993 and Smith-Flueck 2003).

The population from which our males were sampled originated from the animals released at Peninsula Huemul. Today’s distribution of free-ranging red deer covers a long north to south stretch of the Andean-cordillera ecotone, ranging from the lenga forest to the west and reaching out into the steppe to the east (Flueck *et al.* 1995, 2003), with numbers estimated at more than 100 000 individuals in Patagonia (Flueck *et al.* 2003). In the favourable ecotonal habitat, densities recently reached a high of 100 deer/km² (the present study area) and 40–50 deer/km² in the steppe (Flueck *et al.* 2003), being several fold higher than densities recorded for Scottish deer on the Island of Rhum (Clutton-Brock *et al.* 1982, p. 268).

Besides an Austrian–Hungarian heritage, the red deer in this area have also been shown to contain genes identified specifically with North American wapiti or elk (*Cervus elaphus canadensis*), which would have already been present in the first red deer imported from Europe 100 years ago (Flueck and Smith-Flueck 2011). The importation of American wapiti to Europe is well documented, with individuals brought to Austria, Poland and Hungary over 250 years ago to improve trophies for sport hunting. For one example, several hundred wapiti individuals were said to have been introduced to Austria by the Emperor Franz Josef (1830–1916) where they hybridised with the native red deer (Whitehead 1993). Introductions of wapiti were primarily into deer parks from where subsequent introductions were made into wild populations (Pérez-Espona *et al.* 2011). The wapiti, although currently classified as the same species as red deer (Nowak and Walker 1999), has a few phenotypic characteristics that make it easily discernible from its European relative; these include larger body size (twice to three times that of the Scottish red deer), an antler rack of greater size, weight, and a different form and easily distinguishable male rut calls. The wapiti rut call is known as a *bugle*, whereas that of the red deer is a *roar*, with the former vocalisation being of a much higher frequency (F0 1–2 KHz; Feighny *et al.* 2006) than the latter (F0 70–162 Hz).

In the present study, we aimed to determine whether free-ranging red deer introduced to the southern hemisphere have

acoustical properties different from those studied in their native range of the northern hemisphere, by describing and quantifying vocalisation characteristics of males during the rutting period. Factors that might be responsible for any possible differences, such as distinct environmental conditions or genetic origins, are discussed.

Materials and methods

The study population inhabits the mountainous ecotone and steppe habitats of the eastern Andean cordillera in the Neuquén province of Argentine Patagonia, where the dominant climate is temperate, with an average of 1200 mm of annual precipitation, mainly falling between April and September. The breeding season, occurring sometime between early March and late April, lasts 3–6 weeks and peaks approximately the last 2 weeks of March. The study area was located on private land within the Nahuel Huapi National Reserve (40°58’S, 71°12’W), at 950-m altitude, less than 20 km from the 1926 release site on Peninsula Huemul. The area over which the rut takes place is characterised by a mosaic of habitats, with the open mallins being the predominant habitat used by prime stags to set up their territories for retaining harems; the habitats include the following:

1. Forest patches – represented by a variety of pure and mixed stands of *Nothofagus antarctica*, *Austrocedrus chilensis*, *Lomatia hirsuta*, *Maytenus boaria* and *Schinus patagonicus*.
2. Brush patches – represented predominately by *Berberis* spp., *Colletia spinosissima* and *Rosa mosqueta*.
3. Mallins – a type of wet grassland; common throughout the eastern cordillera of the Andes, which is defined as exhibiting running water or inundated soils all year round. Cyperaceae, Juncaceae and other wetland species dominate the wet central sections of the mallins. Of the graminoides, *Carex canescens* and *C. macloviana* (Cyperaceae) and *Juncus depauperatus* are the most prevalent species. The dryer outer edge of the mallin has more xeric graminoid and forb species, such as *Festuca pallescens*, *Hordeum chilense*, *Poa* spp. and *Ranunculus peduncularis*.
4. Grass-dominated steppe – represented by *Stipa speciosa* var. *major* and *Festuca pallescens*, with a variable occurrence of brush species such as *Mulinum spinosum*, *Berberis* spp. and *Colletia spinosissima*.
5. Riparian – a habitat with *Salix* sp. and *Nothofagus antarctica* as the predominant species.

The recordings were conducted during the peak of the rutting period (20–26 March 2007), predominately during the height of daily activity (approximately from sunrise to 1100 hours, and from 1630 hours to sunset). For the seven identified males recorded, behavioural records were taken as well as photographs. Four of these were dominant breeders, each of which held a territory with seven or more hinds present. Throughout the peak period of the rut, focal stags remained the entire day in their established territories in the open mallins, leaving only if disturbed. Whereas these dominant stags often bedded down in the open in the heat of the day, the females, in contrast, often left to bed in the cover of the brush and forest patches on the nearby hillsides. Throughout the day, the males would continue to call, even while bedded, although sporadically and with less intensity.

An occasional intruding male was cause for the bedded stags to rouse, concomitantly increasing the frequency of their calls. The roaring activity picked up again in the late afternoon, stimulated by hinds returning to the mallin, although timing varied daily according to the meteorological conditions (Smith-Flueck and Flueck 2006).

The recordings of the vocalisations were made with a TCD 5M portable recorder (Sony Corporation), type II cassettes and a unidirectional microphone (Audio-technica AT835b, frequency response = 20 – 20 000 Hz) with a wind damper. The maximum recording distance was 100 m. The tapes were then digitalised with Spectrogram 14 (Visualization Software LLC, sample rate: 11 kHz, 16 bit, FFT 512, frequency resolution 21.5) and acoustic characteristics (duration, low frequency and high frequency) analysed with Raven Pro (Cornell Lab Ornithology, Ithaca, NY). For formant and pitch analysis we selected 37 common roars from the seven identified males and we extracted filter formant-related acoustic features with Praat 5.1.37 DSP package (P. Boersma and D. Weenink, University of Amsterdam, The Netherlands). To characterise the filter, we measured the lowest frequency values for the first eight formants and the minimum spacing between them (Min ΔF), using the formant command in Praat (edit, formant, show formants). Parameters for the formant analysis were maximum formant frequency = 2000 Hz, number of formants = 8, and window length (s) = 0.1. In some cases, the lowest frequency formants were not visible or the values obtained were higher than expected for the first formant. In these cases, by comparing the formant values from Praat with the formant means and ranges obtained by Reby and McComb (2003a), we then determined whether this value was the first or second formant; i.e. if the first formant indicated by Praat was 390 Hz, this value is closer to the second formant in Reby and McComb (2003a), and thus was interpreted as such. In these cases, we did not put a value for the first formant, and instead used only the higher formants. We determined the relationship between ΔF and VTL using the formula given by Reby and McComb (2003a). We plotted the formant values as a graph of frequency (kHz) v. formant spacing (ΔF). A linear regression line was then fitted and the slope of this regression was used as the best estimate of Min ΔF , according to Reby and McComb (2003a).

Since the F0s in many vocalisations were not visible, we estimated the values by means of a calculation. In harmonic sounds, the harmonics are integer multiples of F0 and thus the spacing between harmonics permitted us to estimate F0. First, we measured the frequencies at the 5th harmonic visible using Spectrogram 14. Then we measured the spacing between the five harmonics visible in each roar for each male; we averaged these values and obtained one mean F0 value for each male. With the values of F0 for each male, we calculated the mean for our study population which we then compared with red deer data from the Island of Rhum (Scotland).

Results

Of the 731 vocalisations recorded, we were able to analyse only 91, for the others were not clear enough, containing too much noise either from wind interference or overlapping vocalisations from nearby males. From the spectrograms, three principal types of vocalisations were identified. These were mainly distinguished

by their structure and total duration in seconds (Table 1), and are listed below.

1. Common roar (Fig. 1): a harmonically structured sound, with well defined tones and formant frequencies. This vocalisation had the greatest spectrographic variability, because some common roars had many harmonics and others had atonal parts (both at the beginning and at the end of the call); these vocalisations were emitted both in bouts and in isolation.
2. Harsh roar (Fig. 2): a chaotic structure, with some areas of greater intensity within its frequency range. This vocalisation was produced both in bouts and in isolation.
3. Bark (Fig. 3): this, the shortest vocalisation, showed an atonal structure, and was produced either in a rapid series, or as single barks.

The most common vocalisation for all deer recorded was the common roar (47%), followed by the harsh roar (28%) and the least common was the bark (25%) (Table 1).

In addition, from the common roars sampled ($n = 37$) from seven identified stags, we obtained average values for the mean fundamental frequency, Min ΔF and Max VTL (Table 2), and then compared these values with those obtained for red deer in their native northern hemisphere range (Table 3; Fitch and Reby 2001; Reby and McComb 2003a). Although we did not know the ages of our recorded males, the calculations obtained for ΔF and Max

Table 1. Mean (\pm s.e.) values for duration, minimum frequency and maximum frequency in Patagonian red deer vocalisations

Call	<i>N</i>	Duration (s)	Minimum frequency (Hz)	Maximum frequency (kHz)
Common roar	37	1.430 \pm 1.90	183 \pm 16	2828 \pm 125
Harsh roar	31	0.650 \pm 0.70	89 \pm 17	2706 \pm 140
Bark	23	0.230 \pm 0.10	133 \pm 26	2538 \pm 249

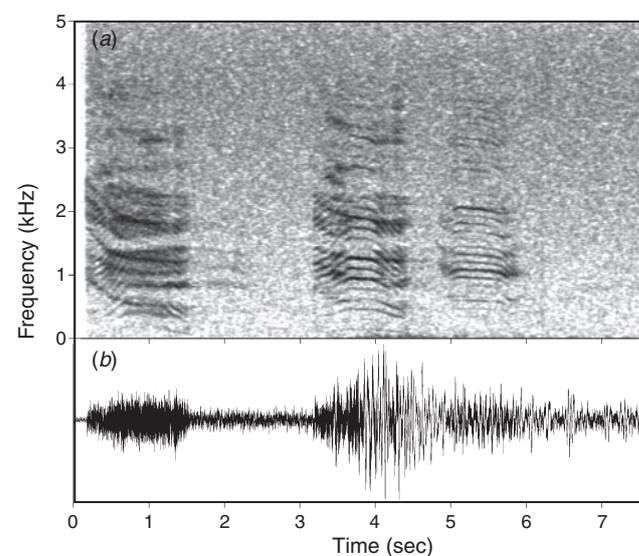


Fig. 1. Bout of common roars. (a) Spectrogram (frequency vs time); (b) oscillogram (amplitude vs time) (from Praat software, see text for details).

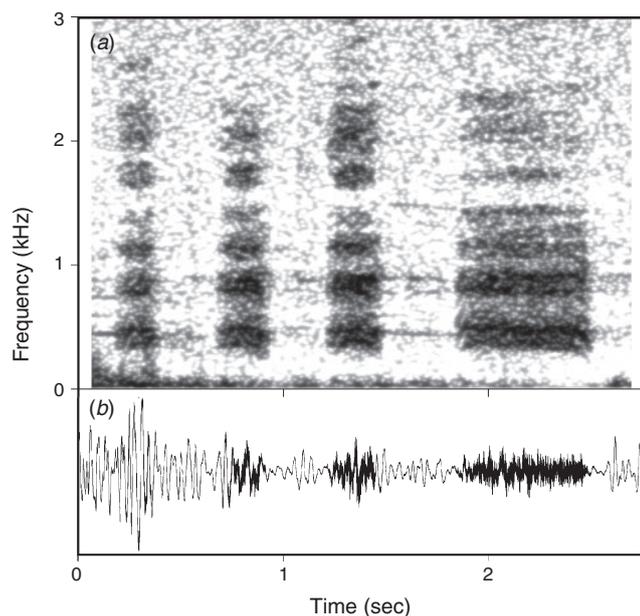


Fig. 2. Bout of harsh roars. (a) Spectrogram (frequency vs time); (b) oscillogram (amplitude vs time) (from Praat software, see text for details).

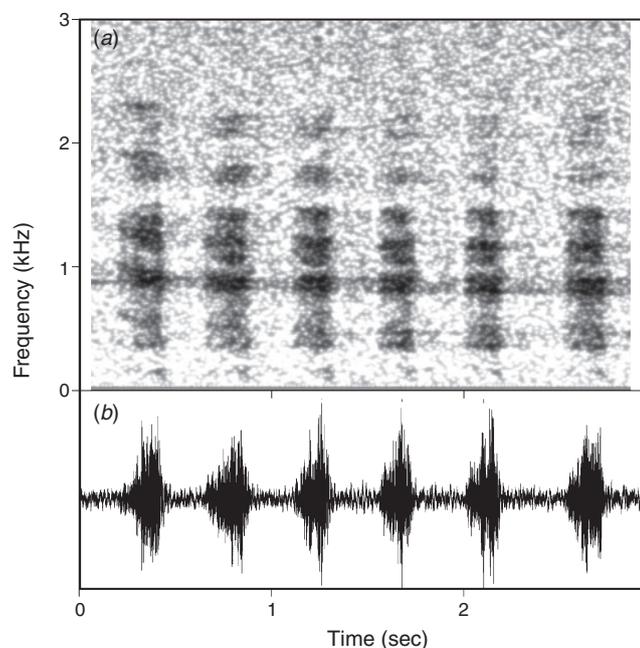


Fig. 3. Bout of chase bark. (a) Spectrogram (frequency vs time); (b) oscillogram (amplitude vs time) (from Praat software, see text for details).

VTL allowed us to identify them as adult males by comparing them with values from Reby and McComb (2003a), in which the ages and weights of the Scottish stags were recorded. The four males in our study area with the highest VTL values (73.5 cm, 71.6 cm, 73.1 cm and 72.2 cm) were also the males with the largest antler racks, containing 11–14 points (M2, M4, M6 and M7, respectively) and had harems with hinds at the time of recording. The remaining three males had adult, but smaller, values of

Table 2. Mean values for fundamental frequency and formant frequency in Patagonian red deer vocalisations for seven identified males F0, fundamental frequency; ΔF , formant spacing; Min ΔF , minimum spacing between formants; MaxVTL, maximum vocal tract length

Individual (<i>n</i>)	Fundamental frequency	Formant frequency	
	Mean F0 (Hz)	Min ΔF (Hz)	MaxVTL (cm)
M1 (7)	140.4	254.1	69.3
M2 (6)	139.6	238.5	73.5
M3 (4)	142.6	250.0	70.4
M4 (5)	123.0	244.4	71.6
M5 (3)	138.6	245.6	71.3
M6 (3)	116.8	239.3	73.1
M7 (9)	120.7	243.0	72.2
Mean	131.7	245.0	71.6

Table 3. Comparative mean values of maximum vocal tract length (Max VTL) and fundamental frequency (F0) from three populations of red deer

Red deer	MaxVTL (cm)	F0 (Hz)
Scottish (Reby and McComb 2003a)		
Subadults	65.1	125.1
Adults	71.9	106.9
Total mean	70.6	111.7
Nahuel Huapi National Reserve		
Without harem	70.3	140.5
With harem	72.6	125.0
Total mean	71.6	131.7
French (Fitch and Reby 2001)		
Males	74.3	

VTL (69.3, 70.4 and 71.3 cm), and lacked hinds at the time of recording (Table 2). The mean Max VTL was comparably larger and mean F0 was higher for red deer males from the Nahuel Huapi National Reserve than for males from Scotland (Table 3).

Discussion

From our recordings of the vocalisations produced by red deer stags (*Cervus elaphus*) in the study area of Nahuel Huapi, the reproductive calls were found to be similar to their native European counterparts in that we could identify the three main vocalisations as for the deer of the Island of Rhum in Scotland (Reby and McComb 2003a, 2003b). Although some red deer from Nahuel Huapi have a genetic component from wapiti (*Cervus elaphus canadiensis*), with the superoxide dismutase allele typical for wapiti found to occur in 11% of animals in the present study population (Flueck and Smith-Flueck 2011), these deer have roars typical of red deer. The bugle, which is the rut vocalisation characteristic of wapiti (Feighny *et al.* 2006), was never apparent in any of the vocalisations recorded. Moreover, during our study period, which fell during the rut peak (J. M. Smith-Flueck, unpubl. data), the common roar was the most frequently produced vocalisation. Harsh roars during this time period were mainly observed in agonistic interactions between stags and alternated with common roars.

Reby and McComb (2003b) described two types of barks distinguished by their behavioural context, namely, the isolated

bark, or single bark, which is directed to a stationary female, and the serial bark, which corresponds to the chase bark, emitted by stags when chasing a female or a competitor. In addition, in the Nahuel Huapi population, the single bark has also been observed in males (1) when trying to get a stationary female in their harems to move and (2) when suddenly faced with an unknown disturbance. The chase bark is frequently used by a territorial male when chasing a juvenile male out of his territory (J. M. Smith-Flueck, unpubl. data).

The common roar was the vocalisation most observed in previous acoustical and statistical analyses (McComb 1987; Reby *et al.* 2001, 2010; Reby and McComb 2003a; Charlton *et al.* 2007, 2008). Bouts of common roars permit individual identification (Reby *et al.* 2006). The application of source-filter theory to red deer common roars showed that minimal formant frequency dispersion, in general, is negatively correlated with body size, and, thus, is an honest indicator of fighting ability (Reby and McComb 2003a; Reby *et al.* 2005). In red deer, minimal formant frequency dispersion is also a good indicator of age (decreasing with age) and is positively correlated with reproductive success (Reby and McComb 2003a). During the emission of the common roar, the stag raises its head and stretches its neck, inducing a descent of the larynx, which decreases the ΔF and the minimal formant frequencies, and increases the VTL.

We found that the four males with the lowest ΔF and the longest calculated VTLs were the only identified males holding harems, which is in agreement with the findings of Charlton *et al.* (2007). Using playbacks of common roars re-synthesised to indicate longer VTLs and thus larger body size; those authors determined that hinds prefer males whose roars have formants with lower minimum frequencies and ΔF . Another study of male behaviour during the rut on this same Nahuel Huapi population showed only males of larger body mass and antlers with a greater number of points defending and holding territories and females that chose to remain in those territories (Smith-Flueck and Flueck 2006).

In our data, the male with the lowest F0 is not the male with the highest value of VTL (and therefore, the largest body size), because F0 is not a good indicator of body size (Reby and McComb 2003a). Although the mean F0 and male quality are not correlated, F0 is higher in the roars of subadults than in those of adult stags (Reby and McComb 2003a) and thus potentially can act as an additional cue to the maturity of the stags (Charlton *et al.* 2008). Recent studies in which the authors used playback of re-synthesised roars with very high and very low F0s within the natural range have also found that oestrous red deer hinds prefer stags with higher minimum F0s, so that sexual selection could be acting to raise the F0 (Reby *et al.* 2010). The mean values of F0 for our population (Table 2) were higher than the values obtained previously for adult males (7–13 years old) and closer to the values for subadult red deer (5–6 years old, Reby and McComb 2003a). In our results, the stags with harems had lower F0s than did males without harems (Table 3), in contrast to the results of Reby *et al.* (2010) described above; however, the sample size in our study was too small to draw conclusions.

The results of the present study have shown that an exotic European red deer population separated from Europe for over a century has vocalisation patterns almost indistinguishable from

those of the native red deer. The fact that the F0s observed in the Patagonian red deer are somewhat higher than those observed in the red deer from Rhum (Reby and McComb 2003a) may indicate a genetic influence of wapiti on the roars, given that Patagonian red deer do have some wapiti genetic markers (Flueck and Smith-Flueck 2011). Playback experiments in captive females of red deer have demonstrated that sometimes females preferred mating calls of heterospecific males (*Cervus nippon*) to those of conspecific males (*Cervus elaphus*), in spite of the acoustic and spectrographic differences between the two (Wyman *et al.* 2011). Wapiti have much higher F0s (0.41–1.9 kHz) (Feighny *et al.* 2006) than do native European red deer. Although wapiti have also been introduced in the past two centuries to Great Britain (Whitehead 1993), deer from the Scottish highlands were shown to have little introgression of haplotypes from wapiti when analysing a paternally inherited genetic marker on the Y chromosome (Pérez-Espona *et al.* 2011), indicating that exotic wapiti there seem to have had little impact on the genetic make-up of the Scottish Highland red deer. In contrast, we might explain the notably stronger wapiti influence on the genetic make-up of the Nahuel Huapi population by the fact that the founder population started with 20 individuals that are likely to have had a high percentage of wapitoid genes, reflecting the history of numerous wapiti introductions to Austria. Also, with few founders in Patagonia, substantial dilution over the past century would not be expected.

Another explanation for the higher F0s in the calls of the Patagonian red deer might be related to the different mating strategies utilised, which in turn could be influenced by environmental factors (Carranza *et al.* 1995; Putman and Flueck 2011). The dominant males of the present study population display territoriality (Smith-Flueck and Flueck 2006), in contrast to prime males in Scotland defending mobile harems (Clutton-Brock *et al.* 1982). Factors that alone or in combination could affect mating strategies include habitat quality, population density, sex and age composition, and genetic make-up of the population. Further comparative studies of red deer vocalisation might aim to elucidate the factors responsible for the variation observed in F0s between the populations of the northern and southern hemispheres.

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