

Spectral acoustic structure of barking in roe deer (*Capreolus capreolus*). Sex-, age- and individual-related variations

Structure acoustique spectrale de l'aboiement chez le chevreuil (Capreolus capreolus). Influence du sexe, de l'âge et différences inter-individuelles

David Reby*, Bruno Cargnelutti, Jean Joachim, Stéphane Aulagnier

Institut de recherche sur les grands mammifères, Inra, BP 27, 31326 Castanet-Tolosan cedex, France

(Received 20 August 1998, accepted after revision 21 December 1998)

Abstract – In roe deer, barking is a loud call commonly given by males and females during inter- or intraspecific interactions. The analysis of a set of 19 spectral variables computed on 560 calls revealed significant variation between sexes, individuals, and probably age classes. Discriminant analysis predicted the sex of an individual with a 93.5 % probability from a small portion of the bark frequency range. Among six males, a linear combination of six variables predicted the identity of the barking individual with a 70 % probability. These sexual and individual differences provide the potential for social recognition from vocalizations. These results are consistent with the hypothesis that barking in roe deer may allow remote signalling of presence, location and identity, and play an important role in the territorial system of this species. (© Académie des sciences / Elsevier, Paris.)

individual vocalizations / acoustic communication / deer / *Capreolus capreolus*

Résumé – Les chevreuils mâles et femelles émettent des aboiements lors d'interactions inter- ou intraspécifiques. L'analyse d'un jeu de 19 variables spectrales démontre l'existence de variations entre les sexes, les individus, et probablement entre les classes d'âge. Une analyse discriminante portant sur une petite portion de l'étendue fréquentielle de l'aboiement permet de prédire le sexe d'un individu avec une probabilité de 93,5 %. Parmi six mâles, l'identité de l'émetteur d'un aboiement peut être déterminée avec 70 % de succès, à partir d'une combinaison linéaire de 6 des 19 variables spectrales. Ces différences sexuelles et individuelles constituent un potentiel de reconnaissance sociale à partir des vocalisations. Ces résultats sont cohérents avec l'hypothèse selon laquelle chez le chevreuil, l'aboiement permet un signalement à distance de la présence, de la localisation et de l'identité de l'émetteur, jouant ainsi un rôle important dans le système territorial de cette espèce. (© Académie des sciences / Elsevier, Paris.)

signature vocale / communication sonore / cervidés / *Capreolus capreolus*

Note communicated by Pierre Buser

* Correspondence and reprints: dreby@toulouse.inra.fr

Version abrégée

Les chevreuils émettent des aboiements puissants et répétés lorsqu'ils perçoivent un élément inhabituel dans leur environnement. L'aboiement est émis en direction de la source de dérangement, probablement afin qu'un prédateur potentiel soit informé du fait qu'il a été détecté et qu'il renonce à poursuivre son attaque. L'aboiement est également émis lors d'interactions intraspécifiques, et peut provoquer l'émission d'aboiements en réponse chez les chevreuils voisins. Il est particulièrement fréquent chez les mâles adultes en période de territorialité. Il est donc probable que cette vocalisation joue un rôle de communication intraspécifique, permettant aux animaux de s'identifier et de se localiser à distance en milieu forestier. Une telle forme de reconnaissance sociale sonore implique que l'aboiement soit vecteur d'information sur le statut de son émetteur (sexe, âge, identité...). L'objet de cette étude est donc l'analyse de la structure acoustique de cette vocalisation, dans le but de caractériser la nature et la stabilité de ses sources de variation, et donc son potentiel informatif.

Nous avons enregistré les aboiements de neuf femelles, trente et un mâles adultes et deux mâles de 1 an pour comparer la structure acoustique des aboiements des deux sexes. Afin de rechercher des différences interindividuelles, nous avons également enregistré pendant deux printemps consécutifs 45 séries d'aboiements de sept mâles identifiés d'âge connu (deux subadultes, trois adultes et deux âgés).

L'analyse porte uniquement sur la structure spectrale de l'aboiement, c'est-à-dire la répartition moyenne de l'énergie sonore dans le domaine fréquentiel, sur la totalité du signal. Pour chaque aboiement a été calculé un spectre moyen qui génère 32 variables décrivant la répartition (moyenne sur la durée du signal) de l'énergie sonore entre 0 et 5 563 Hz, répartie en 32 bandes de fréquence de 173,9 Hz chacune. Les analyses ultérieures ont porté sur 19 de ces 32 variables. En effet, la première variable (bande de fréquence comprise entre 0 et 173,9 Hz) ne contenait pas d'information propre à l'aboiement, tandis qu'au delà de 3,5 kHz (variables 21 à 32), le signal était généralement très faible et/ou confondu avec le bruit de fond.

Des analyses univariées et multivariées de la variance ont montré qu'il existe des différences significatives entre les deux sexes ainsi qu'entre les individus parmi les mâles. Les femelles émettent des aboiements globalement plus aigus que les mâles. Les aboiements des deux mâles d'un an présentent relativement plus d'énergie dans les hautes fréquences que ceux des mâles et des femelles. Une analyse discriminante avec sélection progressive des variables a permis de prédire le sexe d'un individu avec 93,5 % de succès à partir de l'analyse de trois des dix-neuf variables spectrales issues d'un de ses aboiements. Les aboiements des deux mâles yearlings sont reconnus comme étant émis par des mâles. Le même type d'analyse conduite sur les séries d'aboiement émises par six des sept mâles étudiés a permis d'identifier l'auteur de la série dans près de 70 % des cas à partir de six des dix-neuf variables. Les erreurs de classification entre mâles ont principalement lieu au sein des subadultes ou au sein de l'ensemble « adultes et âgés » (4 ans et plus). Cela suggère qu'il existe des différences entre les classes d'âge au sein d'un même sexe, mais que ces différences ne masquent pas l'information liée au sexe.

Ces différences entre classes de sexe, d'âge et entre individus reflètent probablement des différences de taille corporelle entre mâles, femelles, jeunes et adulte, ainsi qu'une variabilité interindividuelle de la morphologie de l'appareil phonatoire. Il est peu probable qu'elles jouent un rôle dans les relations interspécifiques. En effet, il n'y a pas de raison pour qu'une proie potentielle ait intérêt à signaler son sexe, son âge ou son identité à un prédateur. Il est en revanche fortement probable que, chez cette espèce forestière dont les mâles sont territoriaux, de telles informations permettent aux animaux de signaler à distance leur présence et leur identité, particulièrement lors des sessions d'aboiements impliquant plusieurs individus. Une suite logique à cette étude serait donc l'exploration en milieu naturel de cette fonction probable de l'aboiement, au moyen d'expériences de rediffusion faisant varier le statut (sexe, âge) du récepteur et de l'émetteur des aboiements, et leur degré de familiarité (voisin versus inconnu).

1. Introduction

Roe deer emit short, loud and repeated barks when they detect something unusual in their environment [1]. Barking is mainly associated with inter-specific disturbance context: in a recent study, Reby et al. (submitted paper) suggested that roe deer bark toward the source of disturbance to advertise their awareness of danger, and therefore deter the predator's hunting. However, barking often elicits counterbarking among neighbouring individuals and barks are also emitted during intraspecific interactions [2]. Moreover, barking is more frequently observed in bucks and during the territorial season, suggesting that it may secondarily play a role in the territorial system of

this species. Territorial males may signal their presence when barking at a disturbance, and identify and localize conspecifics (male or female, neighbour or stranger, young or adult) during barking/counterbarking session. However, such a role for barking is highly underlain by the existence of potential recognition cues for sex, age and even individuality within its acoustic structure.

In this study, we analyse the acoustic structure of roe deer barks in the frequency domain, in order to extract the potential sources of variation in this vocalization that could represent recognition cues. We also discuss the potential role of these variations in the social and spatial organizations of roe deer.

2. Material and Methods

2.1. Study area and animals

The study was carried out in the 600-ha Fabas forest, near Toulouse, south-west France (43° 21'N, 0° 51'E). It is a mixed forest of oak (*Quercus sp.*), fir (*Abies sp.*), pine (*Pinus sp.*) and hornbeam (*Carpinus betulus*). We could observe roe deer at an average distance of 35 m (Leica Vector 1500 DAE rangefinder binocular; A.J.M. Hewison, unpublished data), but this distance varied from < 5 m in dense understory of coppice regrowth to > 100 m in stands of mature pine. An extensive network of roadways and trails afforded excellent access throughout the study area.

Roe deer is a small-bodied cervid living in predominantly wooded habitats. During winter, roe deer gather in small groups corresponding to family units (a buck, a doe and up to three fawns) [3]. Adult bucks are territorial from March to end of August, the rut takes place from mid-July to mid-August, and they litter from mid-May to mid-July [4].

In our study area, roe deer were free-ranging and regularly hunted between September and January. In winter 1997, population density was estimated at 23 deer/100 ha on a 150-sample plot located within the study area using capture-mark-recapture techniques [5].

2.2. Data collection

Data were collected during spring 1997 and 1998. Four transects were regularly walked within a 300-ha area. During these transects, roe deer barked in reaction to our presence. We recorded all the barking series, determining whenever possible the sex and age classes of the emitter. Barking series from undetermined individuals were not considered. Three age/sex classes were identified: females, adult males (> 2 years) and yearling males (1–2 years). Yearling females could not be reliably distinguished from adults. As roe deer were not individually identifiable, some individuals may have been recorded more than once during the study. However, given the size of the study area and its high roe deer density, we assume that the probability of recording the same individual more than once is low enough to consider the recorded barking series as originating from different animals. To compare spectral characteristics between males and females, we randomly selected one bark per recorded series of each

unmarked male and female. We therefore analysed nine barks from nine unmarked females and 31 barks from 31 unmarked adult males. We also considered five barks from two unmarked yearling males, but this sample was insufficient to constitute a representative category.

We captured and radiocollared three bucks in 1996 and five in 1997. The age class of the marked bucks (yearling, subadult: 2–4 years, adult: 4–6 years, or old: 7 years and more) were approximated from the examination of tooth wear [6] (*table 1*). The radiocollared bucks were regularly and intentionally disturbed to provoke and record barking. For this experiment, the observer radio-tracked the animal so as to approach as close as possible, until the animal fled and/or barked. We recorded the vocalizations of seven of the radiocollared males (the yearling never barked). To compare spectral characteristics between individual males, we considered 515 recorded barks (45 series) emitted by these seven marked bucks (*table 1*).

2.3. Signal recording and processing

During transects and approaches, barks were recorded at distances ranging between 20 and 50 m from the animals, using a Telinga pro-III-S /DAT microphone (frequency band from 100 to 15 000 Hz \pm 6 dB) and DAT Sony TCD D-7 recorders (amplitude resolution: 16 bits, sampling rate: 48 kHz). Numerical sound files were imported on a Macintosh Quadra 950 via an Audiomedia 2 sound card and Sound Designer software. Sound files were converted at an 11.127-kHz sampling rate (8 bit amplitude resolution). Recordings with a relatively high level of background noise were rejected from the data set.

In order to visually examine the spectral dynamics of barking, sound files were transferred to SoundEdit software and intermediate band spectrograms (176.5-Hz filter bandwidth) were produced.

2.4. Spectral analysis of signals

In order to calculate the Average Power Spectrum (APS) of each vocalization [7, 8], we performed a fast Fourier transform (FFT size = 64, overlap P = 50 %, frequency resolution = 173.9 Hz, Hanning window function) on the total length of each signal. The transform output generated 32 variables, which represent the distribution of sound energy over the duration of the signal for each of 32 inter-

Table 1. Distribution of the recorded barking series from the seven marked roe deer bucks considered in the study.

Bucks	Age in 1998	Weight (kg)	Series	Barks
1	4–6	24.2**	6	35
2	2–4	22.1**	4	29
3	2–4	20.4**	10	159
4	4–6	23.2*	2	38
5	> 6	24.2**	6	33
6	4–6	20.5**	8	105
7	> 6	24.3*	9	116

*Weight in 1996; **weight in 1997.

vals of 173.9 Hz (the power spectrum is normalized and transformed into dB). These 32 variables (F1–F32) average the distribution of energy in the frequency domain over the total length of the signal. This computation eliminates the temporal size of the signal. Although duration, amplitude and frequency modulation may also encode individual or sex/age class characteristics, these features are not considered in this study.

2.5. Statistical analyses

We analysed variability of the APS within and between sex classes by performing univariate and multivariate analyses of variance, and discriminant function analyses. All tests were processed using the DISCRIMINANT command of SPSS Professional statistics 6.1 [9]. Significance was accepted at an alpha level of 0.05. For all discriminant analyses, a stepwise selection algorithm was applied to the APS variables set in order to select the variables that were necessary to achieve discrimination. This procedure has already been applied for discrimination of categories in vocalizations [10–13]. The criteria used for variable selection was the minimization of Wilk's Lambda (F to enter = 2.0, F to remove = 1.5). In each discriminant analysis, two classification results were considered: the percentage of original barks that were correctly classified (resubstitution), and the percentage of cross-validated barks that were correctly classified ('leave-one-out' procedure). Cross-validation indicates the model's ability to predict membership of new barks.

Using the stepwise discriminant function calculated for the sex factor, the 515 barks from the seven marked bucks and the five barks from the two unmarked adult yearlings were tested as additional cases ('hold out' procedure).

Barks emitted in a series are more likely to be homogeneous than barks from different series, and therefore not statistically independent [14]. In order to compare the variation attributable to individuals, series within individuals and barks within series, we performed univariate nested analyses of variance (SPSS GLM and VARCOMP syntax commands, DESIGN: individual, series (individual)) on the APS set variables from barks of the marked males.

At last, multivariate and classification analyses were performed on the 45 barking series. Each series was characterized by the mean of each of the 19 APS variables from all the barks it included, in order to leave intra-series variation aside and to avoid pseudo-replication. We conducted a stepwise discriminant function analysis on 43 barking series from six bucks (with two series only, buck no. 4 was not considered).

3. Results

3.1. Spectral structure

Sonograms of typical male and female barks are presented on *figure 1*. Barks are harsh, noisy calls with no

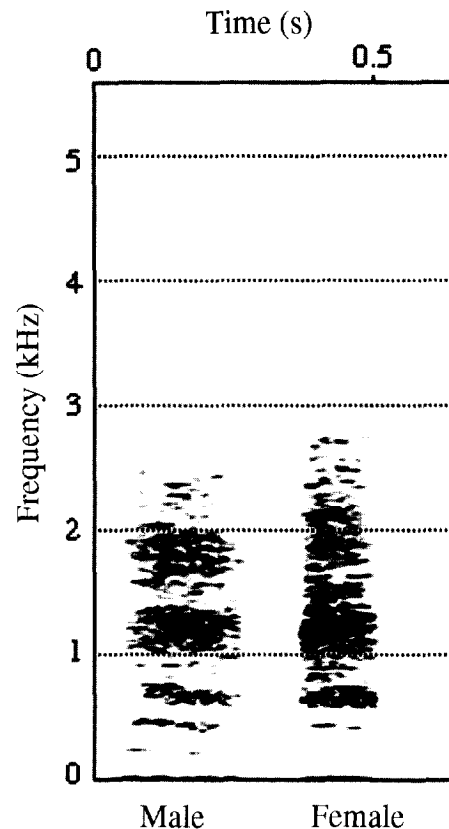


Figure 1. Typical sonograms of male and female roe deer barks. Barks are noisy, atonal calls.

apparent pitch structure. The frequency range is 200–4 000 Hz, with 95 % of relative energy (in dB, as calculated from the APS variables) concentrated in this band. Moreover, above 3 500 Hz, the bark often disappears behind low level background noise. Therefore, F1 variable and F21–F32 variables were not considered in the analyses. The retained band (0.2–3.5 kHz/F2–F20) accounted for 90 % of the signal's energy.

3.2. Differences between sexes

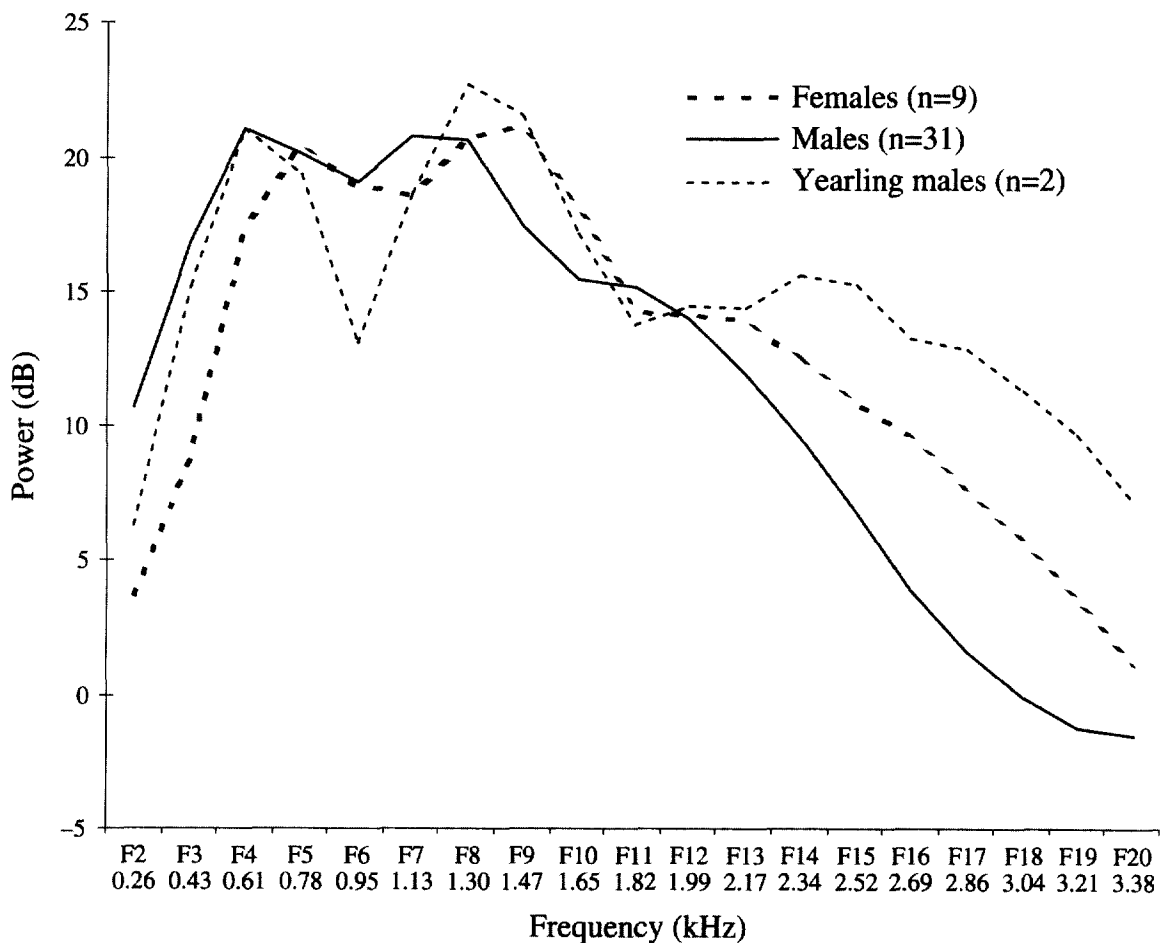
The multivariate analysis showed that the barks APS sets were significantly different between sexes (Wilks lambda = 0.001; $F = 2.505$; $df = 19, 20$; $P = 0.024$). From F2 to F20, 10 of the 19 variables were significantly different between sexes (*table II*). Globally, the male bark concentrated significantly more energy than the female bark in the low frequencies and significantly less in the high frequencies (*figure 2*). Though our sample is small, yearling male barks tend to concentrate more energy in the high frequencies than barks from adult females and males.

The linear factorial discriminant analysis computed on APS values 2–20 correctly classified 95.0 % of the resubstituted barks according to their sex (80.0 % for cross validation). The discriminant stepwise procedure selected APS variables F3, F7 and F8. Other variables were

Table II. Tests of equality of means performed on the 19 average power spectrum variables from male ($n = 31$) and female ($n = 9$) roe deer barks.

Variable	Female		Male		Test	
	mean	SD*	mean	SD*	F	P
F2	3.55	4.71	10.65	4.81	17.486	0.000
F3	8.76	4.81	16.86	4.44	31.264	0.000
F4	17.31	4.44	21.04	3.84	9.772	0.003
F5	20.38	3.84	20.13	4.71	0.052	0.821
F6	18.92	4.71	19.01	3.10	0.008	0.927
F7	18.55	3.10	20.77	3.77	4.625	0.038
F8	20.64	3.77	20.57	3.05	0.004	0.948
F9	21.13	3.05	17.39	2.09	6.777	0.013
F10	17.95	4.71	15.45	2.49	3.477	0.070
F11	14.19	2.49	15.13	2.95	0.500	0.484
F12	14.05	2.95	13.92	4.03	0.014	0.905
F13	13.84	4.03	11.86	4.86	2.721	0.107
F14	12.42	4.86	9.55	4.73	3.040	0.089
F15	10.84	4.73	6.73	4.42	4.530	0.040
F16	9.64	4.42	3.87	3.54	8.013	0.007
F17	7.48	3.54	1.57	3.68	10.082	0.003
F18	5.63	3.68	-0.11	3.80	10.228	0.003
F19	3.46	3.89	-1.20	4.18	5.903	0.020
F20	1.02	4.71	-1.52	4.42	1.591	0.215

Variables in bold are significantly different between sexes. *Standard deviation.

**Figure 2.** Average power spectrum profiles of adult males ($n = 31$), females ($n = 9$) and yearling males ($n = 2$) roe deer barks.

Females barks are higher pitched than males barks, as they concentrate relatively less energy in the low frequencies and more in the high frequencies. Yearling males barks concentrate more relative energy in the high frequencies than adult males and females.

Table III. Variance component estimates (Var) due to individuals, series within individuals and barks within series for each of the APS variables from 515 barks uttered in 45 series by seven individual roe deer bucks.

Variable	Individuals		Series		Barks
	Var	P	Var	P	Var
F2	14.1	0.006	28.5	0.000	3.5
F3	10.0	0.000	9.1	0.000	3.3
F4	0.5	0.311	11.4	0.000	3.7
F5	0.9	0.141	5.9	0.000	3.0
F6	5.0	0.002	7.8	0.000	2.8
F7	3.2	0.137	22.8	0.000	2.8
F8	17.6	0.001	25.9	0.000	3.5
F9	13.8	0.001	19.6	0.000	3.4
F10	7.0	0.031	22.3	0.000	4.8
F11	9.6	0.027	29.3	0.000	6.4
F12	18.1	0.004	33.6	0.000	6.1
F13	27.2	0.001	36.7	0.000	6.5
F14	34.7	0.000	31.7	0.000	9.1
F15	33.7	0.000	33.6	0.000	11.1
F16	21.1	0.006	41.3	0.000	12.7
F17	9.9	0.058	40.3	0.000	13.8
F18	4.9	0.160	38.2	0.000	14.7
F19	4.6	0.161	36.1	0.000	16.6
F20	6.3	0.079	29.1	0.000	18.0

Variables in bold are significantly different between individuals.

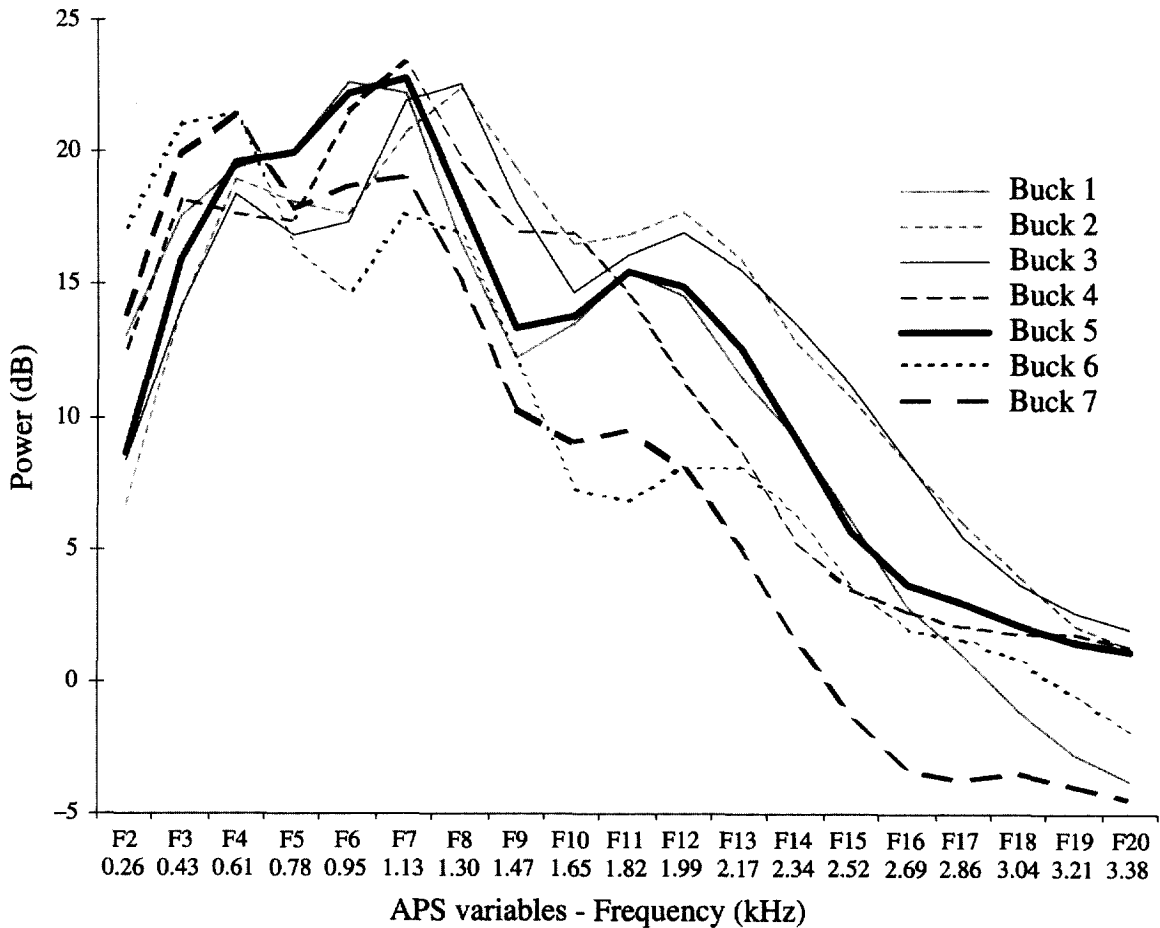


Figure 3. Average power spectrum profiles of barking series emitted by seven individual bucks from three different age classes. Profiles are variable between individuals. Though the sample is small, subadult barks tend to be higher pitched than those of adults and old individuals.

Table IV. Confusion matrix of the discriminant function cross-validation performed on the APS variables F2, F5, F6, F7, F11 and F14 of 43 barking series from six individual roe deer bucks.

Individual	Predicted group membership						% correct	N
	Subadults		Adults		Olds			
	2	3	1	6	5	7		
2	4	0	0	0	0	0	100	4
3	1	8	1	0	0	0	80	10
1	0	0	3	0	2	1	50	6
6	0	0	0	7	0	1	87.5	8
5	0	1	1	0	4	0	66.6	6
7	0	1	0	1	3	4	44.5	9

Total correctly classified: 69.8 %.

rejected because they were highly correlated with F3 or because they were poor predictors. The discriminant function yielded 95.0 % of correct classification in resubstitution and 92.5 % in cross validation. Though correct classification percentages in resubstitution slightly decreased after the stepwise selection of variables, cross-validation percentages increased. This suggests that the discriminant function computed with all the variables integrated information not relevant for the model. A discriminant analysis performed with F3 only (173–346-kHz band) allowed 82.5 % of correct classification (resubstitution).

The discriminant function computed with F3, F7 and F8 classified 80.0 % of the 515 barks from the seven marked bucks as male barks (82.2 % of the 45 series). Individual scores ranged from 58.0 to 97.4 %. Lastly, the five barks from the two yearling males were classified as being male.

3.3. Differences between bucks

The univariate (*table III*) nested variance analyses showed that most APS variables varied significantly between individuals and that series were highly variable within individuals, whereas barks within series were rather homogeneous. From F2 to F20, 12 variables were significantly different between the individuals.

Spectrum profiles of barking series were significantly variable between individuals (*figure 3*, Wilks lambda = 0.001; $F = 2.298$; $df = 114, 122.5$; $P < 0.001$). The linear factorial discriminant analysis correctly classified 97.7 % of the 43 series from the six individuals in resubstitution and 41.9 % in cross validation. The stepwise procedure selected six variables (F2, F5, F6, F7, F11, F14) for 81.4 % of correct classification for resubstitution and up to 69.8 % (versus 16.6 % from random expectation) for cross-validation (*table IV*). The examination of the confusion matrix shows that, while individuals are correctly discriminated within age classes, most misclassifications (80.0 %) occur within subadults or within adult and old bucks.

4. Discussion

4.1. Acoustic structure of barking

In a wooded environment, the frequency window for optimal sound propagation lies between 1 600 and 2 500 Hz [15]. The roe deer bark concentrates 30 % of the relative energy in this band, confirming that it is efficient for long distance communication. In mammals and birds, noisy, wide band calls are generally more readily localized than narrow band or pure tones calls [16, 17]: barks may be designed to be easily localized, contrarily to most single-note alarm calls that are featured to prevent the caller location. This is coherent with some other results showing that barking is not an alarm call, but rather a pursuit-deterrent signal (Reby et al., submitted paper).

4.2. Sex-, age- and individual-related variations

The spectral structure of roe deer barks is sexually dimorphic, female barks being globally higher pitched than those of males. This difference is marked enough to reliably predict the sex of a roe deer from the 174–346-kHz frequency band of its bark. This confirms our field observations when we rarely misidentified the sex from an individual from the pitch of its barks. Though the barks of the yearling males generally sound higher pitched than those of adult males, they are correctly classified as being males by the male–female discriminant function. This is probably due to the fact that the discriminant uses the low frequencies (F3, F7 and F8), where adult and yearling males have comparable spectra. Therefore, age-related variations do not mask sex-related differences.

In adult males, barks are highly homogeneous within a barking series. Most variations occur between series within individuals and between individuals. Inter- and intra-series variability are most important in the upper frequency spectrum, probably because the energy content of high frequencies is more affected by environmental conditions (distance between the receptor and the source, orientation of the source, background noise, etc.) [18].

The discriminant analysis provided a relatively good prediction of the identity of the author of a bark. Individual differences may partially reflect age-class differences. Indeed, though our sampling of individuals within age-classes was too small to consider the age factor in the nested analysis of variance model, the examination of misclassifications suggests the existence of age-related differences in the acoustic structure of barks.

4.3. Potential biological significance

It has been proposed that natural selection may favour the existence of individual cues in the acoustic structure of social calls for recognition purposes [13, 14]. Our observational and experimental data suggest that barking may only secondarily act as an intraspecific form of communication (Reby et al., submitted paper). In the context of a pursuit-deterrent signal, there is no clear reason why a potential prey would benefit from signalling its sex/age-class membership or identity to the predator. Age and sex differences may simply reflect putative morphological differences. Variation in body size account for a large proportion of pitch variation among monkey species [19], and within males in some anuran species [20]. The observation that vocalizations are higher pitched in females and yearling males than in adult males is consistent with the fact that the sexes are dimorphic in roe deer, and that adult males have larger body sizes [2], and presumably larger vocal tracts.

Individual cues in the frequency domain of vocalizations have been found for the two other studied cervids (red deer, *Cervus elaphus*: [21, 22] and fallow deer, *Dama*

dama [8], as well as in most mammalian species (see [8] for references). This suggests that the presence of individual cues is a general property of mammalian vocalizations, probably underlain by individual morphological variation of the vocal tract [23]. This morphological variation may be functional, but also random and non-adaptive. Therefore, though we cannot exclude that natural selection favoured the existence of variations in the acoustic structure of barking in order to attribute a secondary social recognition function to barking, this hypothesis does not appear to be the most parsimonious.

Whatever the case, the potential for individual, sex and probably age recognition exists in the spectral structure of barking and may play an important role in the sociospatial organization of roe deer, specifically in the territorial system of this species. Whereas remote visual communication is inefficient in closed habitats, and scent marking advertises the long-term presence of territorial individuals [24], barking signals the immediate location of the emitter. As it has been suggested in arctic foxes (*Alopex lagopus*), sex-, age- and individual-related differences may allow mutual identification, particularly during barking/counterbarking sessions [25]. Indeed, preliminary playback experiments have established that territorial roe bucks reacted differentially to the playback of barks from individual bucks of varying age classes. Playback experiments involving barks from several individuals of different age/sex classes and varying degree of familiarity (neighbours/strangers) have to be conducted now in order to assess the real importance of social recognition in roe deer barking.

Acknowledgements: We thank M. Chanal and M. Barreau for allowing us to work in the forest of Fabas and J.M. Angibault for organizing the capture of roe deer. During this study, D. Reby was supported by a grant from Inra, the Office national des forêts, the Fédération des chasseurs de l'Ariège and the Fédération des chasseurs de l'Aude.

References

- [1] Hewison A.J.M., Vincent J.P., Reby D., Social organisation, in: Andersen R., Duncan P., Linnel J. (Eds.), *The European Roe Deer. The Biology of Success*, chapter 10, Scandinavian University Press, 1998.
- [2] Danilkin A., Hewison A.J.M., *Behavioural Ecology of Siberian and European Roe Deer (Capreolus capreolus)*, Chapman & Hall, London, 1996.
- [3] Bideau E., Vincent J.P., Quéré J.P., Angibault J.M., Évolution saisonnière de la taille des groupes chez le chevreuil en milieu forestier, *Rev. Ecol. (Terre Vie)* 37 (1983) 161–169.
- [4] Bramley P.S., Territoriality and reproductive behaviour of Roe deer, *J. Reprod. Fertil. Suppl.* 11 (1970) 43–70.
- [5] Reby D., Hewison A.J.M., Cargnelutti B., Angibault J.M., Vincent J.P., Estimating population size of Roe deer using vocalizations, *J. Wildl. Manage.* 62 (1998) 1341–1347.
- [6] Van Laere G., Boutin J.M., Gaillard J.M., Estimation de l'âge chez le Chevreuil (*Capreolus capreolus*) par l'usure dentaire. Test de fiabilité sur des animaux marqués, *Gibier Faune sauvage* 6 (1989) 417–426.
- [7] Joachim J., Lauga J., Populations et dialectes chez le Pinson, *C. R. Acad. Sci. Paris, Série III* 319 (1996) 231–239.
- [8] Reby D., Joachim J., Lauga J., Lek S., Aulagnier S., Individuality in the groans of Fallow deer (*Dama dama*) bucks, *J. Zool., Lond.* 245 (1998) 79–84.
- [9] Norusis M.J., *SPSS Advanced Statistics 6. 1.*, SPSS Inc., Chicago, 1994.
- [10] Sparling D.W., Williams J.D., Multivariate analysis of avian vocalizations, *J. Theor. Biol.* 74 (1978) 83–107.
- [11] Snowden C.T., Cleveland J., French J.A., Response to context- and individual-specific cues in Cotton-top tamarin long calls, *Anim. Behav.* 31 (1983) 92–101.
- [12] Macedonia J.M., Individuality in a contact call of the Ringtailed lemur (*Lemur catta*), *Am. J. Primatol.* 11 (1986) 163–179.
- [13] Lengagne T., Lauga J., Jouventin P., A method of independent time and frequency decomposition of bioacoustic signals: inter-individual recognition in four species of penguins, *C. R. Acad. Sci. Paris, Série III* 320 (1998) 885–891.
- [14] Mitani J.C., Gros-Louis J., Macedonia J.M., Selection for acoustic individuality within the vocal repertoire of wild chimpanzees, *Int. J. Primatol.* 17 (1996) 569–583.
- [15] Morton E.S., Ecological sources of selection on avian sounds, *Am. Nat.* 109 (1975) 17–34.
- [16] Hauser M.D., *The Evolution of Communication*, MIT Press., Cambridge, MA, 1996.

- [17] Brown C.H., Auditory localisation and primate vocal behaviour, in: Snowdon C.T., Brown C.H., Petersen M.R. (Eds.), *Primate Communication*, Cambridge University Press, Cambridge, 1982, pp. 144–164.
- [18] Wiley R.H., Richard D.G., Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal communication, *Behav. Ecol. Sociobiol.* 3 (1978) 69–74.
- [19] Hauser M.D., The evolution of nonhuman primate vocalizations: effects of phylogeny, body weight and motivational state, *Am. Nat.* 142 (1993) 528–542.
- [20] Ryan M.J., Constraints and patterns in the evolution of anuran acoustic communication, in: Fritsch B., Ryan M.J., Wilczynski W., Hetherington T.E., Walkowiak W. (Eds.), *The Evolution of the Amphibian Auditory System*, John Wiley Sons, New York, 1988, pp. 637–678.
- [21] McComb K.E., Roaring and reproduction in Red deer, *Cervus elaphus*, Ph.D. thesis, University of Cambridge, 1988.
- [22] Vankova D., Malek J., Characteristics of the vocalizations of Red deer *Cervus elaphus* hinds and calves, *Bioacoustics* 7 (1997) 281–289.
- [23] Tooze Z.J., Harrington F.H., Fentress J.C., Individually distinct vocalizations in timber wolves, *Canis lupus*, *Anim. Behav.* 40 (1990) 723–730.
- [24] Johansson A., Liberg O., Wahlström L.K., Temporal and physical characteristics of scraping and rubbing in Roe deer (*Capreolus capreolus*), *J. Mammal.* 76 (1995) 123–129.
- [25] Frommolt K.H., Kruchenkova E.P., Russig, H., Individuality of territorial barking in arctic foxes, *Alopex lagopus*, in: Klima F., Hofman R.R. (Eds.), *Proceedings of the First International Symposium on Physiology and Ethology of Wild and Zoo Animals*, Z. Säugetierk. Suppl. 2, 1997, pp. 66–70.