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Acoustic monitoring of short-term ingestive behavior and intake in grazing sheep

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ABSTRACT

Acoustic monitoring of the ingestive behavior of grazing sheep was used to study the determinants of intake rate and to estimate dry matter intake (DMI) based on biting and chewing sounds. Each of three crossbred ewes (85 ± 6.0 kg body weight) were tested in 16 treatments resulting from the factorial combination of two forage species (orchardgrass and alfalfa), two levels of biomass depletion (tall = 30 ± 0.79 cm and short = 14 ± 0.79 cm) and four numbers of bites (20, 40, 60 and 80 bites). During each grazing session biting and chewing sounds were recorded with a wireless microphone placed on the ewe's forehead and connected to a digital video camera for synchronized audio and video recording of ingestive behavior. Dry matter (DM) intake rate was higher for alfalfa than orchardgrass (9.4 ± 0.64 *vs.* 7.8 ± 0.58 g/min, $P<0.05$) because of lower fiber content (434 ± 14 vs 558 ± 6.6 g/kg DM, $P<0.01$) and consequently shorter chewing time and fewer chews per unit DM (11 ± 1.0 *vs.* 14 ± 1.0 chews, $P<0.05$) in alfalfa than in orchardgrass. There were no differences in DMI rate between tall and short plants (8.7 ± 0.67 *vs.* 8.5 ± 0.68 g/min, $P>0.05$), because sheep increased biting rate (from 17 ± 1.6 to 28 ± 1.6 bites/min, $P<0.01$) as bite mass declined from tall to short plants (from 0.54 ± 0.02 to 0.31 ± 0.01 g DM, $P<0.01$). Sheep compensated for the reduction in bite mass by allocating fewer chews per bite (from 6.0 ± 0.46 to 3.8 ± 0.47, $P<0.05$) and increasing total jaw movement rate (from 95 ± 6.3 to 122 ± 6.3 movements/min, $P<0.05$). Compound jaw movements (chew-bites) were observed in every grazing session. The number of chew-bites was higher for tall than short plants (0.52 ± 0.05 *vs.* 0.25 ± 0.04 chew-bites/bite, $P<0.05$). The total amount of energy in chewing sound in a grazing session was linearly related to DMI (root mean square error = 6.1 g, coefficient of variation = 27%); 79% of the total variation in total amount of energy in chewing sound was due to *DMI*. Dry matter intake was estimated accurately by acoustic analysis. The best model to predict *DMI* from acoustic analysis had a prediction error equal to 4.1 g (coefficient of variation = 18%, $R^2 = 0.92$). Chewing energy per bite and total amount of energy in chewing sound were the most important predictors because they integrate information about eating time and intake rate of forages. The results demonstrate that ingestive sounds contain valuable information to remotely monitor feeding behavior and estimate dry matter intake in grazing ruminants.

1. Introduction

The ability to accurately and easily measure intake rate of grazing ruminants is important to understand the ecology of grazing systems. Grazing behavior is a critical process linking

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animal productivity, forage resources and animal impact on the landscape (Bullock and Oates, 2000; Laca, 2009). Monitoring and understanding of grazing behavior of ruminants are essential for developing efficient livestock management systems, improving the utilization of pastures and reducing the environmental impact of intensive animal-husbandry practices in the United Kingdom (Gibb, 2006). Livestock grazing behavior can be used to develop grazing systems that are economically and ecologically compatible with conservation of resources (Del Curto et al., 2005).

Acoustical biotelemetry has been used to monitor ingestive bites and chews of cattle (Laca and WallisDeVries, 2000), and to monitor jaw activity and eating time in sheep (Klein et al., 1994) and cattle (Delagarde et al., 1999; Ungar and Rutter, 2006). Acoustic analysis of chewing yields valuable information to quantify ingestive behavior of free-ranging animals (WallisDeVries et al., 1998), grazing dairy cows (Galli et al., 2006b), and stall-fed cattle (Galli et al., 2006a). Energy of chewing sounds was linearly related to forage intake in steers; and dry matter intake (DMI) was predicted accurately based on easily observable behavioral and acoustic variables (Laca and WallisDeVries, 2000; Galli et al., 2006a). Thus, acoustic analysis is a promising method to estimate grazing intake in cattle, and its value depends on the ability to extend it to other domestic ruminants and grazing conditions. In particular, it is necessary to test the generality of relationships between ingestive sound and intake rate across a range of forage conditions.

The aim of the present study was to validate the acoustic monitoring method with grazing sheep in contrasting forage species, herbage availability and structure. Hypothesis were that (1) DMI can be accurately estimated using acoustic measurements of ingestive behavior, (2) there is a linear relationship between DMI and the total amount of chewing sound energy, and (3) energy of chewing sounds per gram of DMI is not affected by changes in forage type or canopy structure that do affect bite mass.

2. Materials and methods

The experiment was conducted at the Sheep Barn of the Animal Science Department of the University of California in Davis, during February and March of 2003.

2.1. Experimental procedure

Treatments consisted of a factorial combination of two forage species, two levels of biomass depletion (heights) and four numbers of bites taken by the sheep. Different forages and canopy heights were used to obtain bites differing in mass and fiber content. Different numbers of bites were used to obtain various DMI levels per session.

Three nonlactating ewes (Rambouillet–Targhee–Dorset–Finn–Polipay crossbred) of 2–4 years of age, weighing 85 ± 6.0 kg, and with experience grazing micro-swards were used. Sheep were fed alfalfa hay ad libitum in a yard near the experimental site and were subjected to a 1-hour fast before measurements.

Alfalfa (*Medicago sativa L.*) and orchardgrass (*Dactylis glomerata L.*) were offered in two plant heights, tall (not defoliated) and short (cut with scissors to approximately 1/2 the height of tall), reproducing two different levels of biomass depletion. Micro-swards were constructed using sods collected daily and secured in plastic pots attached to a baseboard. The assembly represented a small patch where the animal could reach all plants with almost no locomotion (Fig. 1). Plants were obtained from fields at UC Davis, CA. Every morning 50–60 sods of each species were dug from alfalfa and orchardgrass pastures near the sheep barn.

The alfalfa pasture was managed for typical commercial hay production, with flood irrigation and 5–7 cuts per year. The orchardgrass pasture was also flood irrigated and used for rotational grazing with beef cattle. Both forages were in vegetative stage (based on Kalu and Fick, 1981 for alfalfa and Moore et al., 1991 for orchardgrass). Plants that appeared homogeneous in mass and height were selected. Sods were put into pots and brought immediately to the barn where grazing sessions were conducted. The ewes, one at a time, were led to the board with the pots to be grazed. They were allowed to take 20, 40, 60 or 80 bites in four separate grazing sessions. In each session, a number of pots (4, 8, 12 or 16 pots) were simultaneously offered according to the predetermined number of bites. The ewes were controlled with a halter and rope to bring them to the pots and to interrupt the grazing session when the number of bites was completed.

The order of treatments and ewes was randomized. Between eight and nine grazing sessions were conducted each day between 12:00 and 16:00 h during six consecutive days. Randomization was restricted such that the four treatments and the three ewes had to be used at least in one session each day.

2.2. Video and sound recording

Each session was recorded using a standard digital camera (Sony DCR-PC100 digital camcorder). Sounds of biting and chewing were recorded with the same camera using a wireless microphone system (Nady Systems 151 VR). The microphone was pressed against the forehead of the animal by half of a rubber-foam ball fastened to the halter, where the transmitter was attached. A watch with an electronic alarm was attached to the foam and the alarm was set to go off every 10 s. During the six experimental days, the microphones were randomly assigned to the ewes every three days and rotated over the three days.

2.3. Measurements and calculations

Dry matter intake was estimated as the difference between pre and post grazing session forage biomass. Pots were weighed individually with 0.1 g accuracy using a Setra 140 CP digital scale. Two pots per test were weighed before and after each grazing session to estimate evapotranspiration losses. Every day a subset of pots of each species and height were selected at random to measure herbage height in five extended leaves (in orchardgrass) or stems (in alfalfa). Samples representative of the grazed horizon obtained from ungrazed pots were dried at 65 °C, weighed and analyzed for neutral detergent fiber content (NDF, Robertson and Van Soest, 1980).

Sound tracks from videotapes were analyzed using CBTK, a proprietary software for event recognition (Milone et al.,

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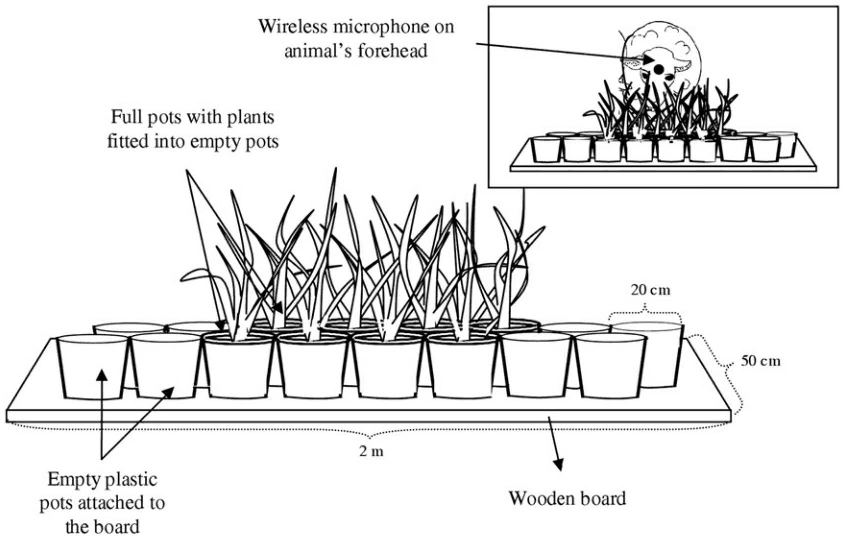

Fig. 1. Schematic illustration of the experimental device.

2009), and Cool Edit Pro version 2 software (Syntrillium Software Corporation, 2002). Sampling rate was 44.100 kHz and sample size (resolution) was 16 bits. The amplitude of digitized signals whose alarm sounds had average amplitude outside the 90 percentile for all alarm sounds was corrected by multiplying it by the ratio between the average amplitude of alarm sound across all recordings over average amplitude of the alarm sound of the session to be fixed. Only five of the 48 signals were corrected in this manner. Alarm sounds were then removed from the recordings. Two sessions in the same day had to be excluded from data analysis because signals were distorted by an unknown source of radio noise.

The number of bites and eating time were determined from sound tracks of videotapes to calculate intake rate (*DMI*/eating time), bite rate (number of bites/eating time) and bite mass (*DMI*/number of bites). Eating time started when sheep apprehended the first bite and finished when she swallowed the last bolus. Bites were identified by the ripping sound produced when sheep sever the forage; chews were identified by the grinding sound of each mastication, and chew-bites were evinced by a chew preceding and partially overlapping a bite within a single jaw movement. Chew-bite sounds are produced when herbage already in the mouth is chewed as the jaws close to sever more herbage.

Chewing and biting sounds were separated and analyzed as in Galli et al. (2005) to obtain the number of bites (B), number chews (C), number of chew-bites (ChB), biting time (TB), chewing time (TC), average intensity (in decibels) of bites (logVB) and intensity of chews (logVC). Then total jaw movements (TJM) was $B+C-ChB$, total jaw movement rate was TJM/T, chew rate (C_T) was C/T, chew per bite was C/B and exclusive chew per bite was $(C-ChB)/B$. Jaw movements that did not produce sound were ignored. The number of chews per g DMI was C/DMI, and the number of chews per g NDFI was $C/NDFI$.

Acoustic energy flux density (EFD) is the product of acoustic intensity and the duration of the sound. In bite and chews, EFD is mechanistically related to the amount of forage severed and crushed. The variables logVB and logVC were measured by the statistics option of Cool Edit Pro, and other variables were calculated as:

$$\text{Biting intensity } \left(\mathrm{W/m^2}\right),\ VB = 10^{(\log VB/10)} \times Iref \quad (1)$$

$$\text{Chewing intensity } \left(\mathrm{W/m^2}\right),\ VC = 10^{(\log VC/10)} \times Iref \quad (2)$$

$$\text{Biting total EFD } \left(\mathrm{pJ/m^2}\right),\ EB = VB \times TB \quad (3)$$

$$\text{Chewing total EFD } \left(\mathrm{pJ/m^2}\right),\ EC = VC \times TC \quad (4)$$

$$\text{Biting duration (ms)},\ TB_B = TB/B \quad (5)$$

$$\text{Chew duration (ms)},\ TC_C = TC/C \quad (6)$$

$$\text{Biting EFD } \left(\mathrm{fJ/m^2}\right) \text{ per bite},\ EB_B = EB/B \quad (7)$$

$$\text{Chewing EFD } \left(\mathrm{fJ/m^2}\right) \text{ per chew},\ EC_C = EC/C \quad (8)$$

$$\text{Chewing EFD } \left(\mathrm{fJ/m^2}\right) \text{ per bite},\ EC_B = EC/B \quad (9)$$

$$\text{Chewing EFD } \left(\mathrm{fJ/m^2}\right) \text{ per unit intake},\ EC_I = EC/DMI \quad (10)$$

$$\text{Chewing EFD } \left(\mathrm{fJ/m^2}\right) \text{ per unit eating time},\ E_T = EC/T, \quad (11)$$

where VB and VC are average intensities in W/m^2 of bites and chews, logVB and logVC are the average intensities in dB of bites and chews, *Iref* is the reference intensity in air (arbitrarily was assumed to be 1 pW in order to have meaningful dimensions), chewing time and biting time are the duration of the signal excluding all “silences” between chews or bites. Chew duration and biting duration are measures of the time during which forage is being crushed

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and severed by the teeth, and is not necessarily a measure of the total time it takes to complete all the jaw motion. For example, total time per chew is composed of chew duration and silence time between chews. Chewing EFD per unit eating time is equivalent to the gross average intensity when the "silences" are included in the signal duration. Formulas 1 to 4 were adapted from Charif et al. (1995). Sounds of bites and chews were described by averaging the spectra of 30 chews and 30 bites.

2.4. Statistical analysis

A mixed model was used for analyses of sound and behavior variables. Fixed effects were forage species (alfalfa vs. orchardgrass), biomass depletion level (tall vs. short), and the interaction between both factors. The random effect was a combination of microphone, animal and day. Increasing the number of bites (20 to 80) results on different *DMI*. By including *DMI* as a continuous covariate, the potential confounding between intake and forage treatments was minimized. A logarithmic transformation of *DMI* (log *DMI*) was used, because when assumptions for *DMI* were verified, the data did not have a normal distribution ($P<0.01$, Shapiro–Wilk test). Forage characteristics were modeled as a factorial of forage species × biomass depletion level with day (from 1 to 6) as a continuous covariable. Differences among least squares means were tested by Tukey–Kramer HSD when effects were significant by the *F*-test. All statistical analyses were performed with JMP® 5.1. software (SAS Institute Inc., 2002). Residuals plots were inspected to check for deviations from linearity and distributional assumptions.

The variables calculated from the sound track measurements were divided into behavior and acoustic variables to compare estimations of intake based on different types of variables. Intake was modeled by multiple linear regression as a function of behavior, acoustic or both sets of variables using variable selection by minimizing the AIC (SAS Intitute Inc., 2002). Models were tested with and without categorical effects for species and biomass depletion.

Path analysis (Li, 1975) was used to evaluate and describe direct and indirect effects of treatments on the intermediate variables and on total chewing EFD. Chewing sound energy was analyzed as a function of its three components measured: chewing intensity, chewing duration and number of chews per g DMI.

3. Results

3.1. Forage

Alfalfa and orchardgrass plants did not differ ($P>0.05$) in biomass or height (Table 1). Dry mass of tall pots was 3.1 times that of short plants (390 vs. 124 g DM/m^2). Height was 30 and 14 cm in tall and short treatments.

Dry matter content was 229 ± 6.6 g/kg and it did not differ ($P>0.05$) among treatments. Fiber content analyses showed interaction between forage species and biomass depletion ($P<0.01$). The NDF content was lower in tall alfalfa than in short alfalfa, but it was not different between short and tall orchardgrass (Table 1).

Table 1
Characteristics of forages used in the experiment.

		Alfalfa	Orchardgrass	Mean
Biomass (g DM/pot)	Tall	14 (1.2)	11 (1.2)	13^a (0.9)
	Short	3.4 (1.2)	4.6 (1.2)	4.0^b (0.9)
	Mean	9.1 (0.9)	7.5 (0.9)	
Height (cm)	Tall	28 (1.1)	32 (1.1)	30^a (0.8)
	Short	15 (1.1)	14 (1.1)	14^b (0.8)
	Mean	21 (0.79)	23 (0.79)	
Dry matter content (DM, g/kg)	Tall	219 (9.3)	242 (9.3)	231 (6.6)
	Short	243 (9.3)	212 (9.3)	228 (6.6)
	Mean	231 (6.6)	227 (6.6)	
NDF (g/kg DM)	Tall	382^c (21)	573^a (19)	477 (14)
	Short	486^b (19)	543^{ab} (19)	515 (14)
	Mean	434 (14)	558 (6.6)	

Values in parentheses are standard errors. Means followed by different letters differ significantly (Tukey–Kramer HSD, $P<0.05$).

3.2. Intake and ingestive behavior

On average, grazing sessions lasted 145 s (between 30 to 506 s), sheep removed 49 bites (between 18 to 86 bites) and consumed 22.4 g DM (between 4 to 62 g). The actual number of bites differed from the nominal treatments because of errors when bites were counted during grazing.

Dry matter intake did not differ ($P>0.05$) between alfalfa (24 ± 2.3 g) and orchardgrass (18 ± 2.3 g), but animals consumed 89% more DM in tall than in short forage ($P<0.01$) with comparable number of bites (Fig. 2). Because of a lower bite mass the slope of the regression of DMI on number of bites was lower ($P<0.05$) for short than for tall plants and also for orchardgrass than for alfalfa. Overall, *DMI* was positively and highly correlated ($P<0.001$) with the number of chew-bites ($r=0.73$), number of bites ($r=0.72$), eating time ($r=0.72$) and number of chews ($r=0.63$). Eating time was more correlated with the number of chews ($r=0.91$) or number of chew-bites ($r=0.86$) than with the number of bites ($r=0.63$).

On average, *DMI* rate of ewes was higher ($P<0.05$) in alfalfa than in orchardgrass, but no differences ($P>0.05$) were detected between tall and short plants (Table 2). Alfalfa

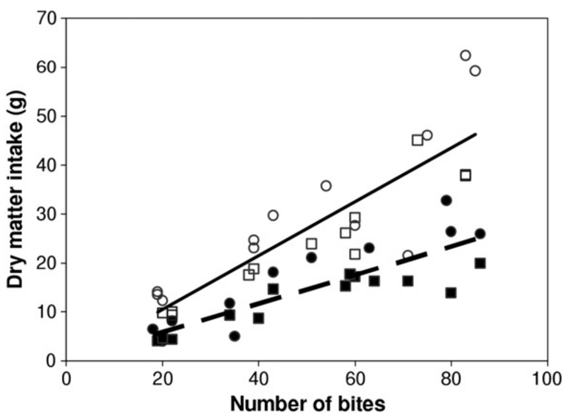

Fig. 2. Dry matter intake as a function of number of bites. Solid line: tall plants, dashed line: short plants, (○): tall alfalfa, (●): short alfalfa, (□): tall orchardgrass, (■): short orchardgrass.

Table 2
Effects of forage species and biomass depletion on ingestive behavior.

		Alfalfa	Orchardgrass	Mean
Intake rate	Tall	9.1 (0.91)	8.2 (0.91)	8.7 (0.67)
(g DMI/min)	Short	9.7 (0.88)	7.3 (0.81)	8.5 (0.68)
	Mean	9.4[a] (0.64)	7.8[b] (0.58)	
Bite mass(g DM)	Tall	0.63[a] (0.02)	0.46[b] (0.02)	0.54 (0.02)
	Short	0.34[c] (0.02)	0.27[d] (0.02)	0.31 (0.01)
	Mean	0.49 (0.01)	0.36 (0.01)	
Bite rate (min^{-1})	Tall	15 (2.0)	18 (1.8)	17[b] (1.6)
	Short	29 (2.0)	28 (2.1)	28[a] (1.6)
	Mean	22 (1.5)	23 (1.4)	
Chews per g DMI	Tall	11 (1.6)	13 (1.5)	12 (1.1)
	Short	10 (1.5)	15 (1.5)	13 (1.1)
	Mean	11[b] (1.0)	14[a] (1.0)	

Values in parentheses are standard errors. Means followed by different letters differ significantly (Tukey–Kramer HSD, $P<0.05$).

yielded larger bites than orchardgrass, particularly in tall plants, resulting in a significant interaction ($P<0.05$). Although bite mass was linearly and positively related with intake rate ($P<0.001$), it explained only 23% of the variance in intake rate. Alfalfa allowed DMI rates 22% greater than orchardgrass ($P<0.05$). Intake rate was not affected by biomass depletion level ($P>0.05$).

Bite rate did not differ between alfalfa and orchardgrass ($P>0.05$), but it was greater ($P<0.05$) in short than in tall plants (28 ± 1.6 vs. 17 ± 1.6 bites/min, Table 2). Orchardgrass required more chews per g DMI ($P<0.05$) than alfalfa (14 ± 1.0 vs. 11 ± 1.0 chews/g DMI), but similar ($P>0.05$) number of chews per g NDFI (26 ± 2.2 vs. 24 ± 2.1 chew/g NDFI).

Table 3
Effect of species and biomass depletion on time per bite and allocation of jaw movements.

		Alfalfa	Orchardgrass	Mean
Time per bite (s)	Tall	4.5 (0.43)	3.9 (0.38)	4.1[a] (0.33)
	Short	2.1 (0.42)	3.3 (0.39)	2.2[b] (0.37)
	Mean	3.3 (0.31)	3.1 (0.29)	
Total jaw movement	Tall	98 (8.25)	92 (7.1)	95[b] (6.3)
rate (min^{-1})	Short	125 (7.80)	117 (7.4)	122[a] (6.3)
	Mean	113 (5.95)	105 (5.6)	
Chewing rate (min^{-1})	Tall	83 (6.5)	92 (5.9)	88[b] (5.1)
	Short	107 (6.5)	101 (6.0)	104[a] (5.2)
	Mean	95 (4.9)	97 (4.6)	
Total jaw movements	Tall	6.5 (0.68)	6.0 (0.60)	6.3[a] (0.48)
per bite	Short	4.3 (0.63)	4.4 (0.62)	4.3[b] (0.47)
	Mean	5.4 (0.45)	5.2 (0.42)	
Total chews per bite	Tall	6.2 (0.62)	5.9 (0.58)	6.0[a] (0.46)
	Short	3.7 (0.61)	3.9 (0.57)	3.8[b] (0.47)
	Mean	4.9 (0.43)	4.9 (0.41)	
Exclusive chews	Tall	5.6 (0.51)	4.3 (0.45)	5.0[a] (0.35)
per bite	Short	3.1 (0.46)	3.4 (0.47)	3.3[b] (0.34)
	Mean	4.4 (0.33)	3.9 (0.32)	
Chew-bites per bite	Tall	0.47 (0.07)	0.57 (0.06)	0.52[a] (0.05)
	Short	0.26 (0.06)	0.25 (0.06)	0.25[b] (0.04)
	Mean	0.37 (0.04)	0.41 (0.04)	
Proportion chew-bite[a]	Tall	0.07 (0.03)	0.10 (0.02)	0.09 (0.02)
	Short	0.07 (0.02)	0.07 (0.02)	0.07 (0.02)
	Mean	0.07 (0.01)	0.08 (0.02)	

Values in parentheses are standard errors. Means followed by different letters differ significantly (Tukey–Kramer HSD, $P<0.05$).
[a] Chew-bites as proportion of total jaw movements.

Taller plants resulted in more time and chewing per bite than short ones, although short plants promoted faster jaw movements (Table 3). Forage species had no effect ($P>0.05$) on time per bite or allocation of jaw movements. Compound jaw movements (chew-bites) were observed in all grazing sessions and were more than double in tall than in short plants.

3.3. Biting and chewing sounds

A typical acoustic signal is shown in Fig. 3 (Top). Each “burst” represents an event (bite, chew or chew-bite). Event duration was between 100 and 250 ms, and there was always a short silence between events, which was also evidenced by the spectrogram in Fig. 3 (Bottom).

Biting sounds were louder (17 ± 0.76 vs. 16 ± 0.78 fW/m^2, $P<0.05$) and shorter (137 ± 11 vs. 216 ± 4.6 ms, $P<0.05$) than chewing events. Biting and chewing sounds differed in spectral composition. Spectra of the different events differed in the bands below 500 Hz (Fig. 4). These differential features are reflected in the time–frequency analysis (Fig. 3b), where bites have more energy below 50 Hz, from 80 to 100 Hz and from 160 to 190 Hz than chews. Chewing sound had more energy from 120 to 140 Hz.

Chewing total EFD was linearly related to *DMI* ($P<0.0001$); 80% of the total variation in EFD was due to variation in *DMI* (Fig. 5). Neither slope ($P>0.05$) nor intercept varied between forages, and the intercepts did not differ from 0 ($P>0.05$). Height ($P>0.05$) and fiber content ($P>0.05$) had no effects on the slope. Treatments did not differ in chewing EFD per g DMI (39 ± 14 fJ/m^2), chewing EFD per unit of time (5.5 ± 0.32 fJ/m^2 s) or chewing EFD per chew (3.4 ± 0.67 fJ/m^2). Tall plants produced more ($P<0.05$) chewing EFD per bite than short ones (Table 4). Alfalfa produced more ($P<0.05$) chewing EFD per g NDFI than orchardgrass.

Chew duration (216 ± 4.6 ms) did not differ ($P>0.05$) among treatments but chewing sounds were louder ($P<0.05$) in alfalfa than in orchardgrass (Table 4). Biting sounds was shorter ($P<0.05$) in orchardgrass than in alfalfa.

3.4. Estimation of intake

Dry matter intake was more accurately estimated by acoustic variables than by behavior variables (Table 5). Furthermore, when the two kinds of variables (acoustic and behavior) were analyzed together, none of the behavior variables were significant, so the best models were the same as those presented for acoustic predictors.

The best models based on acoustic variables included chewing total EFD, biting intensity, chewing EFD per chew and chewing intensity (Table 5). When species and biomass depletion effects were added, chewing EFD per bite replaced biting intensity, chewing EFD per chew and chewing intensity, the R^2 increased to 92% and the CV decreased to 18%. When models with only one predictor were analyzed, chewing total EFD was the best predictor ($R^2=79\%$, $CV=27\%$), the second was chewing time ($R^2=66\%$, $CV=36\%$) and the third, the number of chews ($R^2=47\%$, $CV=44\%$).

When models were based exclusively on behavior variables, only two of fourteen predictors, chewing time and

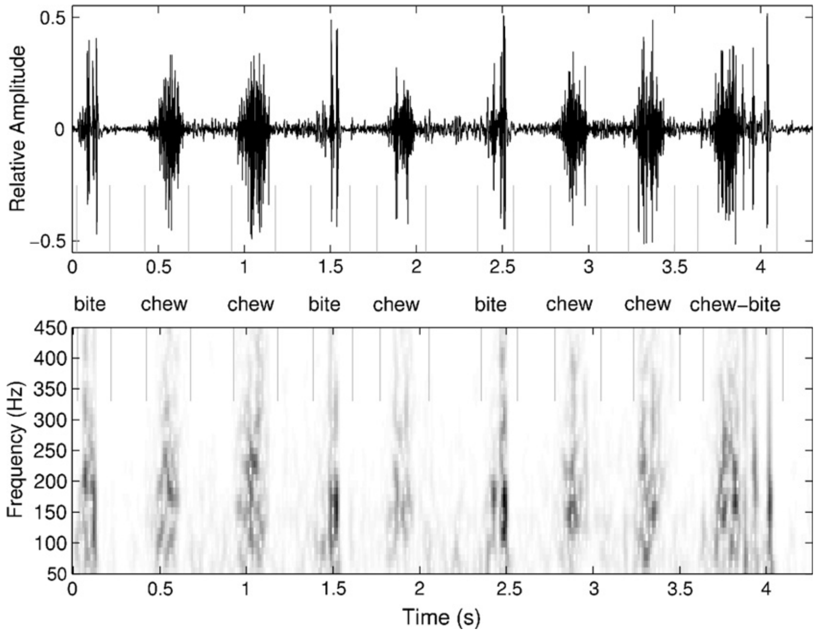

Fig. 3. Top: Fraction of a typical acoustic signal showing a sequence of biting and chewing sounds taken from tall alfalfa plants. Bottom: Time–frequency analysis of the acoustic signal, for each time the spectral content of the signal is showed in gray scale, i.e., the intensity of each point in the image represents amplitude of a particular frequency component at a particular time.

number of chew-bites, contributed significantly to *DMI* estimation (Table 5). Species effects improved the R^2 from 71 to 76% and reduced CV from 36% to 28%, but addition of height did not improve the model.

4. Discussion

This work presents new evidence on acoustic monitoring to ingestive behavior and DMI of grazing ruminants. The method allows accurate measurement of allocation of jaw movement to understand the mechanisms that determine intake. Acoustic monitoring is necessary to identify chew-bites and the results show that chew-bites are relevant to explain intake rate and ingestive behavior in sheep.

4.1. Ingestive behavior

The overall observed results agreed with expectations. There was a positive effect of height on bite mass consistent with previous studies in sheep (Black and Kenney, 1984;

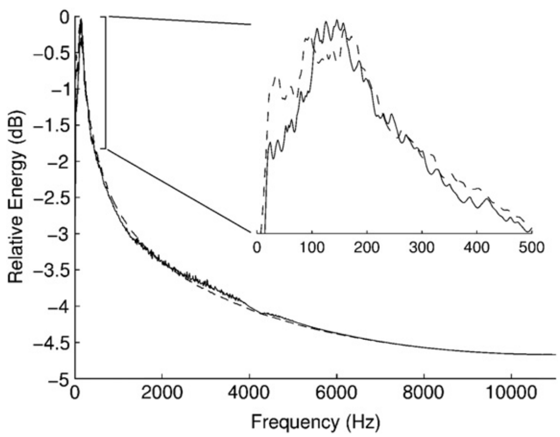

Fig. 4. Spectral analysis of biting and chewing sounds taken from a tall alfalfa plant. Solid line: spectrum average over 30 realizations of chewing sounds. Dashed line: spectrum average over 30 realizations of biting sounds. The section from 0 to 500 Hz is zoomed to show the more important frequency components of the events.

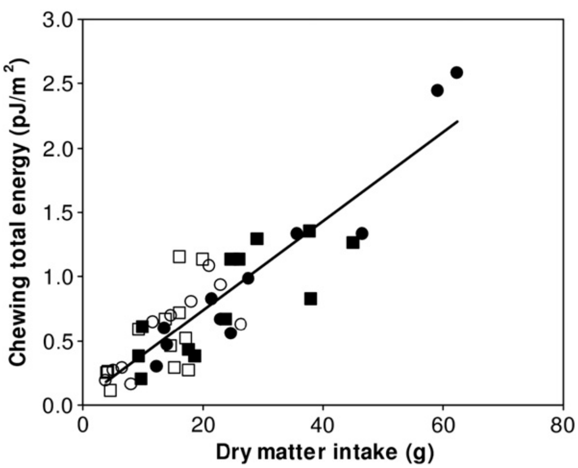

Fig. 5. Relationship between dry matter intake and chewing total energy ($EC = 0.046 + 0.034$ *DMI*, $P < 0.0001$, $R^2 = 0.79$, $N = 46$). Solid line: overall linear regression, (○): tall alfalfa, (●): short alfalfa, (□): tall orchardgrass, (■): short orchardgrass.

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Table 4
Effect of species and biomass depletion on acoustic variables.

		Alfalfa	Orchardgrass	Mean
Chewing EFD (fJ/m^2) per bite	Tall	21 (1.9)	17 (1.7)	19^a (1.4)
	Short	14 (1.9)	12 (1.8)	13^b (1.5)
	Mean	18 (1.4)	14 (1.3)	
Chewing EFD (fJ/m^2) per g NDF	Tall	93 (8.5)	63 (7.6)	78 (6.0)
	Short	85 (8.2)	81 (8.2)	93 (6.1)
	Mean	89^a (5.7)	72 ^{b}(8.2)	
Chewing intensity (fw/m^2)	Tall	18 (1.5)	15 (1.4)	16 (1.2)
	Short	16 (1.5)	15 (1.5)	16 (1.3)
	Mean	17^a (1.2)	15^b (1.2)	
Biting intensity (fw/m^2)	Tall	16^b (1.5)	18^{ab} (1.4)	17 (1.3)
	Short	22^a (1.7)	18^{ab} (1.5)	19 (1.4)
	Mean	19 (1.3)	18 (1.2)	
Biting duration (ms)	Tall	154 (22)	107 (22)	131 (16)
	Short	166 (23)	118 (22)	142 (176)
	Mean	160^a (15)	112^b (15)	

Values in parentheses are standard errors. Means followed by different letters differ significantly (Tukey–Kramer HSD, $P<0.05$).

Burlison et al., 1991; Gong et al., 1996a). Differences in bite mass between plant species are attributed to differences in plant structure. Legumes yield larger bites than grasses (Rogers et al., 1986; Poppi et al., 1987; Gong et al., 1996b; Cangiano et al., 2002).

Ewes were able to maintain intake rate by increasing biting rate when bite mass declined by 50% (Table 2). According to Gibb and Orr (1997) when bite mass decreases, sheep increase bite rate as the need to masticate decreases, maintaining jaw movement rate constant. Under the incorrect assumption that jaw movements are either chews or bites, an increase in bite rate reduces the number of chews per bite. The results in the present work suggest a partially different mechanism. Ewes compensated for the reduction in bite mass not only by allocating fewer chews per bite, but also by increasing total jaw movement (Table 3). Total jaw movement rate (including biting, chewing and chew-biting) and total jaw movements per bite explained 94% of the variation in time per bite.

In agreement with Baumont et al. (2004) the results showed that bite rate and DMI rate are also related to the fiber content of the forage. Dry matter intake rate was greater for alfalfa than orchardgrass. This cannot be attributed exclusively to the larger bites of alfalfa, because intake rate did not respond to even larger changes of bite mass obtained by reduction of herbage biomass. Alfalfa had lower chewing requirements per unit DMI, presumably due to its lower fiber content, and chews per unit of fiber did not differ between plant species. Amount of chewing per unit fiber appears to be a conserved quantity in fresh forages. Overall, ewes chewed 25 ± 1.5 times per gram of NDF, which took 10 ± 0.62 s.

Table 5
Models to estimate dry matter intake based on acoustic or behavior predictors.

Acoustic predictors (p)	Best overall models without species and biomass effects				Best model including species effect	Best model including species and biomass effects
	1 p	2 p	3 p	4 p		
Intercept	2.7	$\underline{11}$	$\underline{10}$	$\underline{12}$	$\underline{13}$	$\underline{12}$
Chewing total EFD	$\underline{23}$	$\underline{23}$	$\underline{22}$	$\underline{23}$	$\underline{22}$	$\underline{25}$
Biting intensity		$\underline{-0.45}$	$\underline{-0.53}$	$\underline{-0.39}$	$\underline{-0.32}$	
Chewing EFD per chew			$\underline{0.86}$	$\underline{1.4}$	$\underline{1.5}$	
Chewing intensity				$\underline{-0.46}$	$\underline{-0.61}$	
Chewing EFD per bite						$\underline{-0.70}$
Alfalfa vs. orchardgrass	–	–	–	–	$\underline{1.5}$	$\underline{1.5}$
Tall vs. short	–	–	–	–	–	$\underline{4.1}$
$\underline{\text{Coefficients}}$						
R^2	0.80	0.85	0.87	0.88	0.89	0.92
R^2adj.	0.79	0.85	0.86	0.87	0.88	0.90
AIC	161	148	146	143	140	132
RMSE (g DM)	6.1	5.2	5.1	4.8	4.7	4.1
CV (%)	27	23	23	21	20	18
Behavior Predictors (p)	1 p	2 p	–	–		
Intercept	3.9	2.7	–	–	2.2	3.1
Chewing time	$\underline{0.32}$	$\underline{0.23}$	–	–	$\underline{0.23}$	$\underline{0.23}$
Number of chew-bites		$\underline{0.31}$			$\underline{0.31}$	$\underline{0.29}$
Alfalfa vs. orchardgrass	–	–	–	–	$\underline{2.9}$	$\underline{2.9}$
Tall vs. short	–	–	–	–	–	$\underline{1.4}$
$\underline{\text{Coefficients}}$						
R^2	0.66	0.71	–	–	0.76	0.77
R^2adj.	0.65	0.69	–	–	0.75	0.75
AIC	176	164	–	–	155	156
RMSE (g DM)	7.9	6.7	–	–	6.1	6.1
CV (%)	36	31	–	–	28	28

N = 46; mean of dry matter intake = 22.4 g, underlined coefficients differ significantly from 0 ($P<0.05$), R^2adj. = R^2 adjusted by p, AIC = Akaike's information criterion, the model that has the smallest value of AIC is considered the best, RMSE = root mean square error, CV = coefficient of variation of prediction. Each column represents the best model with a given number of predictors. Within each column, coefficients are the effects of the predictors on dry matter intake. Coefficients for "Alfalfa vs. orchardgrass" and "Tall vs. short" are the effects of Alfalfa and Tall, respectively, as deviations from the overall intercept. Effects of the alternative level of each factor have the same absolute value with opposite sign.

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In cattle, variation in bite rate was mainly explained by differences in jaw movement allocation rather than jaw movement rate (Laca et al., 1994; Ungar and Rutter, 2006; Ungar et al., 2006). In steers (Laca et al., 1994) and in heifers (Ungar and Rutter, 2006) as the proportion of chew-bites increased, the number of jaw movements per bite declined and therefore the bite rate increased. In the present study, sheep allocated more chew-bites in tall than in short plants and there was no difference between species. Chew-biting reduced the total number of jaw movements per bite without reducing the number of chews per bite. About 50% of the bites in tall and 25% in short plants were simultaneously used for chewing, representing 8.7% of the total jaw movements. These results point out the importance of chew-biting measurements to understand the mechanisms of time per bite and intake rate in sheep.

4.2. Estimation of intake

The present results indicate that it is possible to accurately estimate *DMI* in grazing sheep by acoustic analysis (Fig. 6). Dry matter intake estimations based on acoustic variables were more accurate than model based behavior variables. The number of chew-bites was the only variable that added relevant information to the *DMI* prediction based on chewing time. It appears that the number of chew-bites integrates information about chewing efficiency that is not included in any other variable.

Acoustic analysis allowed accurate estimations of *DMI* in grazing sheep, regardless of the differences on grazing time, bite mass, fiber content, and canopy structure represented in the treatments. The best model had root a mean square error (RMSE) equal to 4.1 g, and the CV was 18%, close to the 16% ($R^2=0.89$) estimated in a previous experiment with steers fed fresh and dry forages (Galli et al., 2006a). The CV of intake estimation by sward cutting techniques varies from 13% on aftermath herbage (cut in the preceding period) to 24% on pastures grazed 2–4 times in the preceding period (Meijs, 1981). The CV of intake estimation is at least 11% to 15% when fecal-index techniques and techniques using fistulated animals are combined with sward sampling for the estimation of feces production (Meijs, 1981).

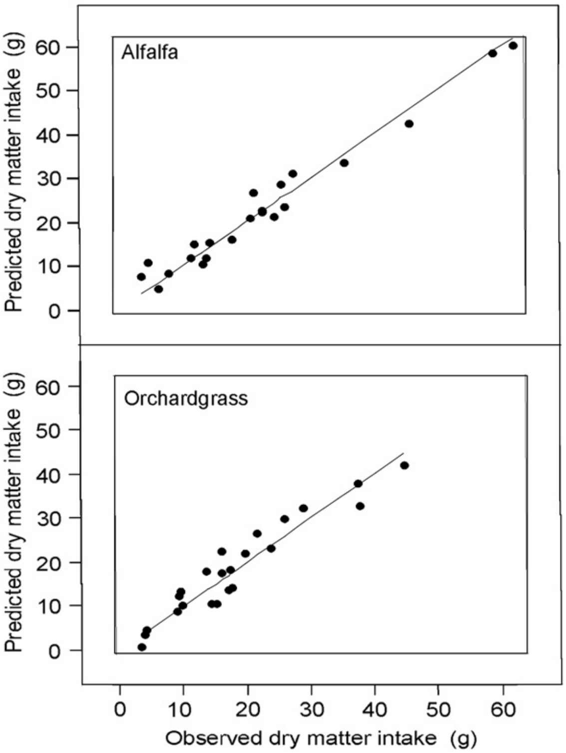

Fig. 6. Relationship between observed and predicted dry matter intake based on acoustic predictors including species and biomass depletion effects ($P<0.0001$, $R^2=0.92$, RMSE = 4.1 g DM, CV = 18%, N = 46). Solid line: y = x.

Chewing sound is not just an indirect measure of grazing time, but it contains substantial additional information related to *DMI*. Chewing energy is central to all models because it integrates information about effective grazing time and intake rate, which is related to chewing energy per unit of grazing time. Chewing total EFD ($R^2=79\%$, CV = 27%) was a better predictor of *DMI* than eating time ($R^2=66\%$, CV = 36%) and than number of chews ($R^2=47\%$, CV = 44%). The chewing energy per unit of grazing time showed a positive overall relationship with intake rate ($P<0.0001$, $R^2=0.33$) and this relationship was maintained ($P<0.0001$, $R^2=0.51$) when species and biomass depletion effects were included in the model.

Energy of chewing sounds was strongly related to the amount of forage ingested in sheep, which is in agreement with results for cattle (Laca and WallisDeVries, 2000; Galli et al., 2006a). As hypothesized, the relationship between chewing total EFD and *DMI* was linear, in spite of the differences of NDF in the forages. Orchardgrass had more fiber than alfalfa, so it required more ingestive chewing than alfalfa, but the chewing sound per g DMI was not different between species.

The sound signal contains information about the intensity and duration of the crushing of forage by the teeth (Laca and WallisDeVries, 2000) that provides a good mechanistic explanation of these experimental results. Energy of chewing sound per unit DMI can be partitioned into three components: chew intensity, chew duration and number of chews per g DMI (Fig. 7). Chews per g DMI was the main component influencing chewing energy and was affected by the forage species. Chewing intensity was also affected by forage species but it had a smaller effect on chewing EFD per unit intake than the number of chews per g DMI. Chew duration was the component with the least influence on chewing EFD per unit intake and it was not explained by any of the controlled experimental factors. Chews per g DMI and chewing intensity, and chews per g DMI and chew duration, were negatively correlated. When the number of chews per g DMI increased, chewing intensity and chew duration decreased. Thus, due to direct and indirect effects, alfalfa and orchardgrass produced comparable chewing EFD per unit intake.

There was a negative relationship between bite mass and chewing per g DMI, apparently related to the increase of efficiency of chewing as larger amounts of forage were retained in the mouth and comminuted per chew. A larger number of chews per g DMI did not increase chewing EFD per unit intake. When more chews per g DMI were applied, the "bursts" were shorter and less intense (Fig. 7), presumably due to the smaller quantity of forage processed in each chew.

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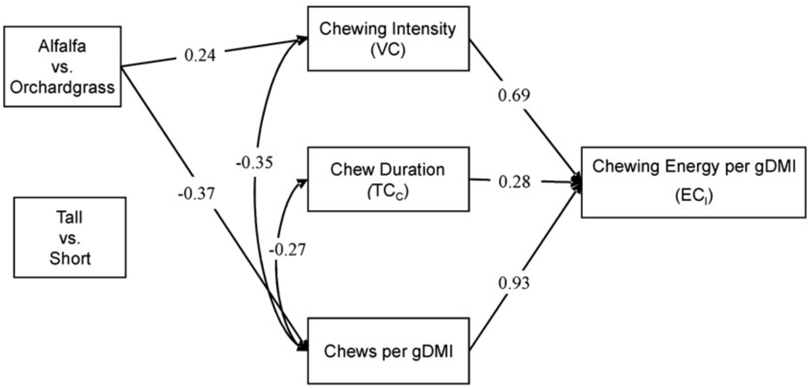

Fig. 7. Path diagram showing how treatments affected components of chewing sound energy per g DMI. Only significant ($P<0.05$) paths are shown. Paths from qualitative variables are given the sign of "Alfalfa" and "Tall". For example, a change from orchardgrass to alfalfa has a positive effect on chew intensity and reduces chews per g DMI. Plant height did not show any significant effect on the explanatory variables. Forage species × Plant height interaction was also considered in the model but the effects were not significant and were not shown in this diagram, for simplicity.

Chewing efficiency decreased and EFD per g DMI increased with decreasing bite mass.

5. Conclusions

This research brings new information to the understanding of the ingestive process in ruminants. Three main mechanisms were involved in mastication effectiveness and chewing behavior in order to attain faster biting rates, (1) increasing jaw movement rates, (2) reducing chews per bite and (3) chewing less per g DMI. Acoustic measurements clearly showed that sheep use jaw movements to simultaneously bite and chew.

Differences between fresh forages did not significantly affect the energy of chewing sound per g DMI. Therefore, chewing total energy appears to be a precise and consistent quantity that can be used for intake estimation.

Ingestive sounds contain valuable information to predict intake and to remotely monitor feeding behavior in free ranging animals. Further work is necessary to automate processing of sound signals and to develop recording systems for the estimation of daily intake.

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