Seasonal variation in rumination parameters of free-ranging impalas *Aepyceros melampus*

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By decreasing particle size of ingested forages, and thereby exposing more surface area to microbial degradation, chewing plays a key role in digestion efficiency in ruminants. However, the investigation of chewing behaviour at a fine scale, and in particular of rumination parameters such as chew number or bolus duration, surprisingly remains limited largely to applied agricultural research. The goal of the present study was to investigate seasonal effects on rumination parameters in free-ranging impalas *Aepyceros melampus*, an African ruminant experiencing a strong seasonality in food quality. Male and female impala increased both chew number and bolus duration in the dry season as compared to the rainy season. This is consistent with previous studies on livestock reporting an effect of food quality on rumination parameters, and with previous work on impala reporting an effect of season on food quality. The coefficient of variation in the chew number increased for both sexes between the rainy season and the dry season, consistent with the greater variability in the food items consumed in the dry season as reported by previous studies. Only males had an increased coefficient of variation in bolus duration between the rainy season and the dry season. Because females with young may increase chewing investment as compared to dry females in response to energetic costs of lactation, the heterogeneity in reproductive status among females during the rainy season (i.e. rearing period) may have resulted in heterogeneity in bolus duration, thereby interfering with the effect of the variability in the plants consumed. Rumination is an important process that seems to have been overlooked in field studies. Future studies, based on long-term data sets of marked free-ranging individuals should investigate to which extent parameters as easy to record as chew number or bolus duration could be used by managers to assess factors such as food quality and thus, ultimately, population performance in ruminants.

Key words: Aepyceros melampus, bolus duration, chew number, index of nutritional status, rumination at a fine scale, season

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Rumination behaviour is classically considered in behavioural ecology studies investigating activity budgets of free-ranging ruminants: a focal individual is 'ruminating', as opposed, for instance, to 'feeding' or 'being vigilant'. 'Feeding' or 'being vigilant', however, are often further described at a finer scale. Information on bite rate or step rate while feeding (Ruckstuhl 1998, Ruckstuhl et al. 2003) or on scan rate or scan frequency while being vigilant (Hunter & Skinner 1998) is thus widespread in the literature. Contrary to this, very few field studies have investigated rumination at a finer scale, i.e. at the scale of a bolus (e.g. Ginnett & Demment 1997), and in particular in relation to life history strategies of free-ranging animals (e.g. Blanchard 2005). However, by decreasing particle size of ingested forages, and thereby exposing more surface area to microbial degradation (Pond et al. 1984, Pan et al. 2003), chewing plays a key role in digestion efficiency, and in particular during rumination (Trudell-Moore & White 1983, Chai et al. 1984). Accordingly, rumination parameters such as the number of chews per bolus or the bolus duration, have been extensively investigated in agricultural sciences. Numerous studies on livestock reported effects of forage nutritional characteristics on rumination behaviour (Gibb et al. 1999, Tafaj et al. 2005a), and others reported effects of rumination behaviour on digestion efficiency (Domingue et al. 1991). Hence, despite clear evidence for their direct importance in animal feeding biology, the investigation of rumination parameters surprisingly seems limited to applied agricultural research (but see Gross et al. 1995, 1996, Ginnett & Demment 1997, Blanchard 2005).

The goal of our study was to investigate the seasonal effects on rumination parameters in free-ranging impalas *Aepyceros melampus*, a dimorphic African ruminant experiencing a strong seasonality in climate and food quality. We tested two predictions. Forage quality affects rumination parameters (Pérez-Barbería & Gordon 1998). In particular, more fibrous food requires more chewing. Using experimentally controlled diets, several studies on cattle reported a positive influence of fibre content on the chew number and/or on bolus duration (Moon et al. 2004, Tafaj et al. 2005a). Thus, because herbivore diet quality, including that of impalas (Skinner et al. 1983, Meissner et al. 1996), is lower during the dry than during the rainy season, our first prediction was an increase in bolus duration and in the chew number during rumination in the dry season as compared to the rainy season. Impalas are mixed feeders (Hofmann 1989) known to exhibit great dietary flexibility (Meissner et al. 1996, Sponheimer et al. 2003). In the rainy season, impalas mostly graze, whereas their food intake is more balanced between grazing and browsing in the dry season (Skinner et al. 1983, Klein & Fairall 1986, Meissner et al. 1996, Wronski 2002). Because plant characteristics directly impact on rumination parameters, our second prediction was a decrease in the variability in chew number and bolus duration when animals mostly fed on a single type of food, i.e. when grazing during the rainy season. Overall, we thus expected lower average values and lower variability for chew number and bolus duration in the rainy season than during the dry season. If confirmed, these results could promote future applied studies on rumination at a fine scale. A seasonal variation in rumination parameters, suggesting an effect of food quality, is the first step before investigating to which extent inter-year or inter-population fluctuations of food quality, and thus, ultimately, of population performance, may be assessed by variation in chew number or bolus duration. We also recorded the effect of sex on rumination parameters as sexual dimorphism in body size is likely to lead to differences in digestive efficiencies, and thus potentially to compensatory behaviour for the smaller sex (Ruckstuhl & Neuhaus 2002), such as increasing mastication investment (even at an intra-specific scale; Gross et al. 1995, 1996, Ginnett & Demment 1997).

Material and methods

Study area and species

Hwange National Park is located on the north-western border of Zimbabwe (19°00'S, 26°30'E) and covers an area of ca 15,000 km^2. Vegetation is typical of southern African, i.e. dystrophic wooded savannas with patches of grasslands (Rogers 1993). Altitude varies from 800 m to 1,100 m a.s.l. The long-term annual rainfall average is 606 mm with most rain falling between November-April. In the

Hwange system, young impala are generally born around the end of November or early December. Lactation generally lasts until early April, when adult males start to exhibit rutting behaviours that last until early June, with a peak in May. Our study was carried out in the Main Camp region of the park, where impala density is ca 1 individual/km^2 (S. Chamaillé-Jammes, M. Valeix, H. Fritz, M. Bourgarel & S. Le Bel, unpubl. data for the Zimbabwe National Parks and Wildlife Management Authority).

Data sampling

The data were collected in 2005 during two 10-day periods, one during 12-22 February in the rainy season and one during 3-13 September in the dry season. Using 10×42 binoculars, a single observer (PB) performed all the observations from an open-top car. We only focused on adults. Impalas were habituated to cars, and easy to observe. Most of the observations took place from 20-50 m. Focal individuals were chosen according to head orientation, since the face had to be clearly visible in order to record jaw movements. Each observation began with the regurgitation of a bolus chosen randomly, and lasted until the fifth bolus was swallowed. We recorded the amount of time required to process five boli using a stopwatch, and the total number of chews performed during the focal (Blanchard 2005). Observations were discarded if the focal individual stopped chewing for at least five seconds. We also recorded the sex (males have horns whereas females do not).

Individuals were not captured or marked as part of this study. Therefore, as impalas were not individually recognisable, we may have observed the same animal more than once (although not on the same day). We performed a total of 102 observations: 40 and 32 females observed in the rainy and dry seasons, respectively (out of respectively 67 and 63 adult females in the studied population), and 16 and 14 males observed in the rainy and dry seasons, respectively (out of respectively 25 and 24 adult males). Therefore, by observing about the same proportion of individuals for each sex, we avoided increasing the pseudoreplication problem for one sex in respect to the other.

Data analysis

We used linear mixed models (Pinheiro & Bates 2000) to investigate the effects of sex and season on both the number of chews and the time required to process five boli. When finding a group of individuals ruminating, we often performed several observations within the same group. Therefore, we included 'group identity' as a random factor in the analysis in order to control for the non-independence between these observations. To investigate the sources of variation in the number of chews and the total duration of five boli, we first tested the effect of the two-way interaction (sex by season) by testing the difference in log-likelihood between the models with and without the interaction. We then removed the non-significant interaction and successively withdrew each of the two main factors, testing for their significance by comparing the difference in log-likelihood between the models with and without each of the factors.

We compared the variation in rumination parameters using the coefficient of variation (CV), expressed for small samples as $CV = (1 + 1/(4 \times N)) \times (\text{standard deviation/mean}) \times 100$ (Sokal & Rohlf 1995), with N for the sample size. All statistical analyses were done using R software (R Development Core Team 2005).

Results

Average values of rumination parameters

Season clearly affected fine-scale rumination patterns. From the rainy to the dry season, impalas

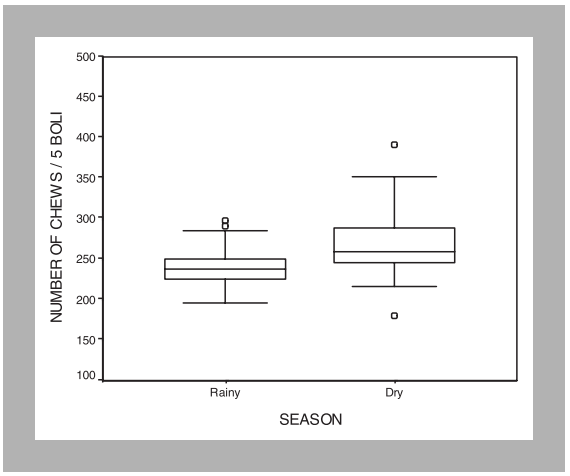

Figure 1. Number of chews performed to process five boli in the rainy (N = 56) and dry (N = 46) seasons, respectively, for impalas observed in Hwange National Park. The line across the box indicates the median. The box represents the interquartile range that contains the 50% of values. The whiskers are lines that extend from the box to the highest and lowest values, excluding outliers. Outliers (values 1.5-3 box lengths from the upper or lower edge of the box) are represented by open circles.

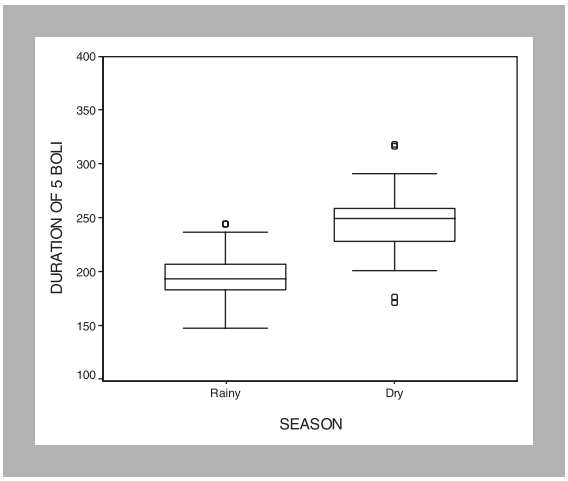

Figure 2. Duration (in seconds) of five boli in the rainy (N = 56) and dry (N = 46) seasons, respectively, for impalas observed in Hwange National Park. The line across the box indicates the median. The box represents the interquartile range that contains the 50% of values. The whiskers are lines that extend from the box to the highest and lowest values, excluding outliers. Outliers (values 1.5-3 box lengths from the upper or lower edge of the box) are represented by open circles.

increased both the number of chews performed per bolus (240.3 vs 268.6 chews for five boli in the rainy and dry seasons, respectively; likelihood ratio = 11.5, difference in df = 1, $P < 0.001$; Fig. 1) and the duration of a bolus (196.1 and 247.0 seconds for five boli during the rainy and dry seasons, respectively; likelihood ratio = 35.0, difference in df = 1, $P < 0.001$; Fig. 2), irrespective of their sex (number of chews for five boli: likelihood ratio = 1.9, difference in df = 1, $P = 0.17$ and interaction sex*season: likelihood ratio = 1.6, difference in df = 1, $P = 0.21$; duration of five boli: likelihood ratio = 2.1, difference in df = 1, $P = 0.14$ and interaction sex*season: likelihood ratio = 0.72, difference in df = 1, $P = 0.40$).

Variability in rumination parameters

The CV in the recorded parameters were affected by both sex and season (Table 1). The CV in the number of chews increased in dry season, as predicted by our second prediction, for males (8.2 and 12.1% in the rainy and dry seasons, respectively) as for females (9.1 and 14.5% in the rainy and dry seasons, respectively). However, sex impacted on the effect of season on the CV of boli duration, with an increase in dry season for males (11.5% as compared to 7.1% in the rainy season), but not for females (12.4% as compared to 12.2% in the rainy season).

Table 1. Coefficients of variation (CV) in the number of chews and the time required (in seconds) to process five boli according to sex and season in impalas, Hwange National Park.

Sex	Parameters	CV for the rainy season	CV for the dry season
Males	Number of chews/five boli	0.082	0.121
	Duration of five boli	0.070	0.115
Females	Number of chews/five boli	0.091	0.145
	Duration of five boli	0.122	0.124

Discussion

Whereas behaviours such as foraging or vigilance are extensively investigated in free-ranging ruminants both at the scale of the time budget and at a finer scale (e.g. records of bite rate or scan rate), rumination at fine scale (i.e. at the bolus scale) remains largely overlooked in literature, despite its particular importance for ruminant feeding ecology. Here, we focused on seasonal variation of rumination patterns in free-ranging impalas. Our data suggest that sex and season impacted on chew number and bolus duration. Male and female impala increased both chew number and bolus duration while ruminating in the dry season as compared to the rainy season, which is consistent with our first prediction based on previous studies reporting a negative effect of food quality on the average values of these rumination parameters (Moon et al. 2004, Tafaj et al. 2005a), and a diet of better quality in the rainy season compared to the dry season for impalas (Skinner et al. 1983, Meissner et al. 1996). Sex had no influence on the average values of chew number or bolus duration. Sexual differences in body size are likely to lead to differences in feeding behaviour, including rumination parameters (Gross et al. 1995, 1996, Ginnett & Demment 1997). However, the sexual dimorphism displayed by our studied animals (about 20%; M. Bourgarel & H. Fritz, unpubl. data) was probably too small compared to those reported by previous studies (about 135% for Nubian Ibex *Capra ibex nubiana*; Gross et al. 1995) to easily detect potential sexual differences in rumination patterns. The CV in the number of chews increased for both sexes between the rainy season and the dry season, whereas only males increased CV in bolus duration. Once again, it is broadly consistent with our prediction that the greater variability in the food items consumed in the dry season (Skinner et al. 1983, Meissner et al. 1996, Wronski 2002) should lead to an increase in the variability in the chew number and in bolus duration from the rainy season to the dry season.

Average values of rumination parameters

Rumination parameters reflect the physical and chemical characteristics of previously ingested forages (Pérez-Barbería & Gordon 1998). In particular, more fibrous forages require higher chewing effort. In an indoor trial conducted with red deer *Cervus elaphus* fed either fresh perennial ryegrass *Lolium perenne* or chicory *Chicorium intybus*, Hoskin et al. (1995) reported higher chewing effort, including chew number, for deer fed with the more fibrous ryegrass. Moon et al. (2004) reported longer bolus duration in dairy cows fed with experimental diets increasing in fibre concentration. Here, we report that both bolus duration and chew number increased in the dry season as compared to the rainy season, irrespective of sex. Impalas are mixed feeders (Hofmann 1989), moving to more woody browse in the dry season, when grass quality becomes too low (Klein & Fairall 1986, Meissner et al. 1996, Wronski 2002). Therefore, the decrease in the quality of the forages ingested by impala during the dry season (Skinner et al. 1983, Meissner et al. 1996) probably results in the longer bolus duration and in the increase in the chew number we report as compared to the rainy season.

Food quality, and in particular fibre content, has also been reported to affect the total time devoted to rumination (Moon et al. 2004), and intake rate may impact on rumination parameters (Bae et al. 1979, Tafaj et al. 2005b). Further studies performed at both fine and large scales for a single population, could improve the understanding of the relationships between food quality, food quantity, time budget and rumination parameters. Further, because many of the indices used by managers to assess nutritional status of free-ranging populations require the capture or the killing of the animal and/or are expensive or irrelevant (Blanchard et al. 2003), future studies should investigate the reliability of rumination parameters in assessing the variability of food quality for a given species according to season, year for a given season, locality or population.

Variability in rumination parameters

We report that season broadly impacted on the variability in rumination parameters, probably explained by a broader range of food items selected in the dry season as compared to the rainy season, as suggested by previous studies (Skinner et al. 1983, Meissner et al. 1996, Wronski 2002). This explanation is also consistent with personal observations in the study area where impalas were mostly seen grazing during the wet season, whereas they relied on more various sources of food in the dry season, including browse and *Acacia* pods but also dried grass, which may form the bulk of their rumen fill. The increase in the variability in the food items consumed during the dry season therefore probably explains the increase in the variability in the chew number reported for both sexes, with more chews being performed when ingesting lower quality items (i.e. lower than the average forage quality, already lower than mean forage quality in rainy season).

The CV in bolus duration was lower in the rainy season than in the dry season for males, as predicted by our second prediction, but the CV in female bolus duration was not affected by season. Females showed about the same variability in both seasons, with more variability than males in the rainy season. Differences in the reproductive status of females may explain this result. Some of the females observed during the rainy season (i.e. the rearing period) were probably lactating while others probably were not (48 juveniles were present in the study area together with a total of 67 adult females in the rainy season). In the dry season, however, all young were weaned so that all adult females had the same status. The heterogeneity in reproductive status in the rainy season may have been translated into a heterogeneity in bolus duration. Blanchard (2005), focusing on the rearing period, investigated variation in rumination parameters as a function of presence/absence of lamb in bighorn sheep ewes *Ovis canadensis*, and suggested that lactating females increased chewing effort, in response to an increased energetic demand and risk of predation, as compared to yeld females. In order to avoid foraging longer than yeld females to meet the energetic costs of lactation, and thus to enjoy the benefit of group foraging (Kie 1999, Sevi et al. 1999) through synchronisation of activities (Ruckstuhl 1998), lactating females may compensate for an increasing intake rate by increasing chewing effort during rumination (Blanchard 2005). In the present study, lactating females may decrease bolus duration as compared to yeld females, in order to process more boli during the same amount of time spent ruminating. This would mean that lactating females increase rumination speed, as reported for bighorn sheep (Blanchard 2005).

Future studies should investigate the impact of reproductive status on foraging behaviour on marked female impalas, as this interpretation remains speculative. Also, if lactating females ruminate faster than yeld females (Blanchard 2005), the CV

in rumination speed among females during the rearing period should crudely scale with the ratio of lactating female to yeld female, i.e. the young: female ratio, an index often used by managers to infer ungulate population dynamics (Bonenfant et al. 2005).

Rumination, particularly at a fine scale, seems to have often been overlooked in field studies. More studies are thus required to improve our understanding of the relationship between rumination behaviour at both large and fine scales (Ginnett & Demment 1997), food characteristics and population dynamics. Because ungulate population dynamics is strongly influenced by changes in density and climatic conditions (Sæther 1997, Gaillard et al. 1998), mostly through their effect on food availability and quality, a proxy of nutritional status would be useful for managers interested in wildlife demography (Blanchard et al. 2003). Future studies, based on long-term data sets of marked free-ranging individuals should investigate to which extent measures as easy to record as chew number or bolus duration could be used to assess factors as important as resource properties and thus, ultimately, population performance in ruminants.

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