On lactation and rumination in bighorn ewes (*Ovis canadensis*)

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Abstract

Because lactation has high energetic costs, females should vary their foraging behaviour according to reproductive status. In ungulates, however, some studies found no differences in feeding behaviour between non-reproductive (yeld) and lactating females. Despite the importance of rumination in determining digestive efficiency, no study has attempted to identify tactics involving this parameter in free-ranging ungulates. Whether or not females varied their ruminating behaviour as a function of the presence/absence of offspring was tested by observing marked bighorn ewes *Ovis canadensis* of known reproductive status, age, and body weight. Lactating ewes ruminated 1.21 times faster than yeld ewes and showed less inter-individual variability in rumination speed, suggesting an energetic constraint. After considering the potential physiological advantages of this behaviour, I suggest that differences in ruminating parameters may allow the synchronization of activities in groups made up of individuals with different energy requirements. Lactating females may increase rumination effort in response to increased energetic demands and risk of predation.

Key words: *Ovis canadensis*, reproductive costs, rumination, predation risks, activity synchrony

INTRODUCTION

The daily energetic requirements of female ungulates may increase by 150% during peak lactation compared to maintenance (Loudon, 1985). It is, therefore, reasonable to expect that the foraging behaviour of females should vary according to reproductive status in order to meet those requirements. As expected, in domestic sheep *Ovis aries* (Penning *et al.*, 1995), cattle *Bos taurus* (Gibb *et al.*, 1999), red deer *Cervus elaphus* (Clutton-Brock, Iason *et al.*, 1982), and bison *Bison bison* (Komers, Messier & Gates, 1993), lactating females spend more time foraging than yeld ones. In addition to spending more time foraging, lactating females could increase food intake through a faster bite rate, as reported for bighorn sheep *Ovis canadensis* in autumn (Ruckstuhl & Festa-Bianchet, 1998), or they could be more selective while feeding, as reported for habitat selection in red deer hinds (Clutton-Brock, Guinness & Albon, 1982; Clutton-Brock, Iason *et al.*, 1982). Although plasticity in foraging behaviour probably reduces the fitness costs of lactation, it often seems to be insufficient to completely compensate

for the increased energy demands: numerous studies have reported evidence of lactation costs for species where reproductive status affects foraging behaviour. For instance, compared to yeld females, lactating females may have lower mass gain, survival or reproduction (Clutton-Brock, Guinness & Albon, 1983; Festa-Bianchet, Jorgensen, Lucherini *et al.*, 1995) or lowered resistance to parasites (Festa-Bianchet, 1989).

Several studies found no differences in the foraging behaviour of female ungulates according to reproductive status (Oakes, Harmsen & Eberl, 1992; Parsons *et al.*, 1994; Pérez-Barbería & Nores, 1996; Toïgo, 1999), including some that also reported evidence of lactation costs (Pérez-Barbería & Nores, 1996). Lack of compensatory feeding behaviour by lactating females may indicate that all females forage at the maximum possible rate. Alternatively, females may also respond to the increased energy cost of lactation by modifying other aspects of their foraging behaviour, such as rumination, or several aspects simultaneously, which makes these tactics more difficult to identify.

In ruminants, chewing is very important for nutrient assimilation (Pérez-Barbería & Gordon, 1998*a*), but no study has assessed the importance of this activity by comparing it to reproductive status in a free-ranging ungulate. By decreasing particle size and thereby exposing

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more forage surface area to microbial degradation (Pond, Ellis & Akin, 1984), mastication accelerates digestion (Bjorndal, Bolten & Moore, 1990). Rumination behaviour may, therefore, affect the proportion of nutrients that are extracted from a given quantity of ingested forage and thus may be involved in tactics aimed at meeting the energetic costs of lactation. For instance, in those studies that report no differences in foraging behaviour according to reproductive status, lactating females may increase intake rate (possibly by modifying parameters that are difficult to assess, for instance bite size), and then increase rumination effort to maintain the digestion rate of the forage ingested. On the other hand, increasing mastication effort may accelerate tooth wear (Gross, Demment *et al*., 1995).

In summer, lactating and yeld bighorn ewes had similar bite rates, step rates (a measure of selectivity; Komers *et al*., 1993), grazing times, and selected the same habitats (Ruckstuhl & Festa-Bianchet, 1998). Lactating ewes gained less mass than yeld ones (Ruckstuhl & Festa-Bianchet, 1998). That study, however, did not examine possible differences in ruminating behaviour. Individually marked free-ranging bighorn ewes of known reproductive status, age and body weight, were observed in order to test the hypothesis that females modify their ruminating behaviour as a function of the presence/absence of offspring.

MATERIALS AND METHODS

Study area and bighorn sheep population

Bighorn ewes *Ovis canadensis* were observed at Ram Mountain, Alberta, Canada (52° N, 115° W) in summer in 1999 and 2000. All ewes were marked and were captured 2–6 times from late May to late September in a corral trap baited with salt. At each capture, reproductive status was classified as yeld, pregnant, or lactating through udder inspection, and ewes were weighed to the nearest 250 g with a Detecto spring scale. All ewes were first marked as lambs and their age was known. Further details about the study area and capture methods are in Festa-Bianchet, Jorgensen, King *et al*. (1996) and in Jorgenson, Festa-Bianchet & Wishart (1993). The Ram Mountain bighorn sheep research protocol was approved by the Animal Care Committee of the Université de Sherbrooke, an affiliate of the Canadian Council on Animal Care (Protocol MFB2 by Marco Festa-Bianchet).

Ewe–lamb pairs were determined by observing marked lambs suckling from marked ewes. Two classes of reproductive status were considered: ewes nursing a lamb (*n* = 15), and yeld ewes (*n* = 18). Not having a lamb can arise as a result of 3 different causes: (1) the ewe was barren (*n* = 5; when examining the udder at capture, neither milk nor colostrum is secreted); (2) the lamb died at or soon after birth (*n* = 10; these ewes were lactating when first captured in late spring but their lamb was never seen); (3) the lamb died during summer (*n* = 3). Because these 3 summer deaths occurred at least 1 month before the ewe's ruminating behaviour was observed, these ewes were

considered as 'yeld'. Excluding them from the analysis led to results similar to those reported here.

Individual rates of mass gain were calculated for ewes caught at least twice with > 30 days between captures (*n* = 30 of 33 ewes). Because ewe mass gain was quadratic (Festa-Bianchet, Jorgenson, King *et al*., 1996), the regression of body mass on the square root of capture date was used to adjust the mass of a given ewe to the day of observation. More details on mass adjustment are in Festa-Bianchet, Jorgenson, King *et al*. (1996). Ewes younger than 5 years were not considered because only 4 of 11 in 1999 and 0 of 8 in 2000 reproduced.

Observations

The ewes were habituated to people and easily observable. Most observations took place from 30–100 m, using a spotting scope (25–40 × 60, Bushnell). Once a bolus is regurgitated, the ewe typically chews it for slightly < 1 min, then performs about 5 rapid jaw movements before swallowing. All the observed ewes had moulted, so that both regurgitation and swallowing were easily observable because of the short neck hair.

Focal observations (Altmann, 1974) began with the regurgitation of a bolus chosen randomly, and lasted until the tenth bolus was swallowed. The total time and all chews while the 10 boli were processed were recorded using a stopwatch. Observations were discarded if the focal ewe stopped ruminating for > 5 s.

All ewes 5 years of age and older were observed once. The earliest observations took place on 6 July and the latest on 17 September.

Statistical analyses

The influence of reproductive status on rumination behaviour was studied by considering its effect on the relationship between the 2 measured variables, the time required to process 10 boli and the number of chews performed on those boli. Because the number of chews had to be 0 when the processing time was 0, the intercepts were forced through 0. To test for a difference between the slopes according to reproductive status, an F test was used to compare 2 nested models, a model (1) including the difference of slope according to reproductive status in the regression of the number of chews performed for 10 boli on the time required to process these boli *vs* a model (2) including the same slope for both reproductive status in the regression of the number of chews performed for 10 boli on the time required to process these boli.

A previous study found that differences in foraging patterns according to reproductive status only occurred after August (Ruckstuhl & Festa-Bianchet, 1998). Following the first global model where all the data were pooled, the analysis was therefore repeated for observations collected both before and after 1 September.

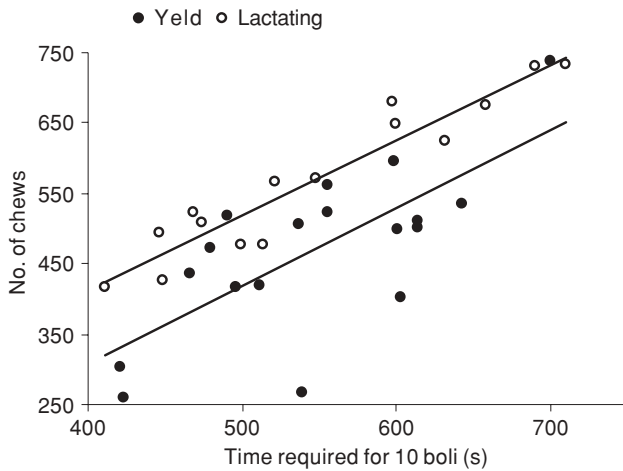Because both body weight and age may affect rumination behaviour (Chadwick, 1983; Pérez-Barbería &

Fig. 1. Number of chews by ruminating bighorn sheep *Ovis canadensis* ewes plotted against the time needed to process 10 boli, with the slopes forced through the origin. For a given processing time, lactating ewes (open circles) had more chews than yeld ewes (closed circles), but less intragroup variability (see also Fig. 2).

Gordon, 1998*a*) and may be correlated with reproductive status in this population (Festa-Bianchet, 1998; Festa-Bianchet, Gaillard & Jorgenson, 1998; Bérubé, Festa-Bianchet & Jorgenson, 1999), 2 1-way ANOVAs were used to check whether ewes differed in age and body weight according to reproductive status.

Not all variables (season, age, body weight, processing time and reproductive status) and not all interactions between continuous variables and factors were incorporated in a single model given the small sample size. Both years were pooled in the analyses since most of the observations took place in 2000 (28 of 33). Means are followed by standard error (SE). All statistical analyses were performed with S plus software (Venables & Ripley, 1999).

Fig. 2. Frequency distribution of rumination speed (chews/s) of bighorn sheep *Ovis canadensis* ewes of different reproductive status: lactating ewes seemed to chew as fast as some physiological constraints allowed them to, whereas yeld ewes showed more inter-individual variability.

RESULTS

Ewes with and without a lamb did not differ in age (mean of 8.9 and 9.7 years, respectively; $F_{1,31} = 0.61$, $P = 0.44$) or body weight (mean of 66.6 and 69.6 kg, respectively; $F_{1,28} = 2.47$, $P = 0.13$).

Lactating and yeld ewes had different rumination patterns. The F test between the two nested models was highly significant ($F_{1,31} = 18.21$, $P < 0.001$), so model (1), including a difference between the slopes according to reproductive status, was the most appropriate. The slope forced through the origin (i.e. the rumination speed, expressed as chews/s) was much higher for lactating than for yeld ewes (1.04 ± 0.015 compared to 0.86 ± 0.035; Fig. 1). Lactating ewes ruminated on average 1.21 times faster than yeld ewes.

For a given processing time, lactating ewes clearly showed less inter-individual variability than yeld ewes in the number of chews (Fig. 1). Lactating ewes may have chewed at a rate near their physiological constraint,
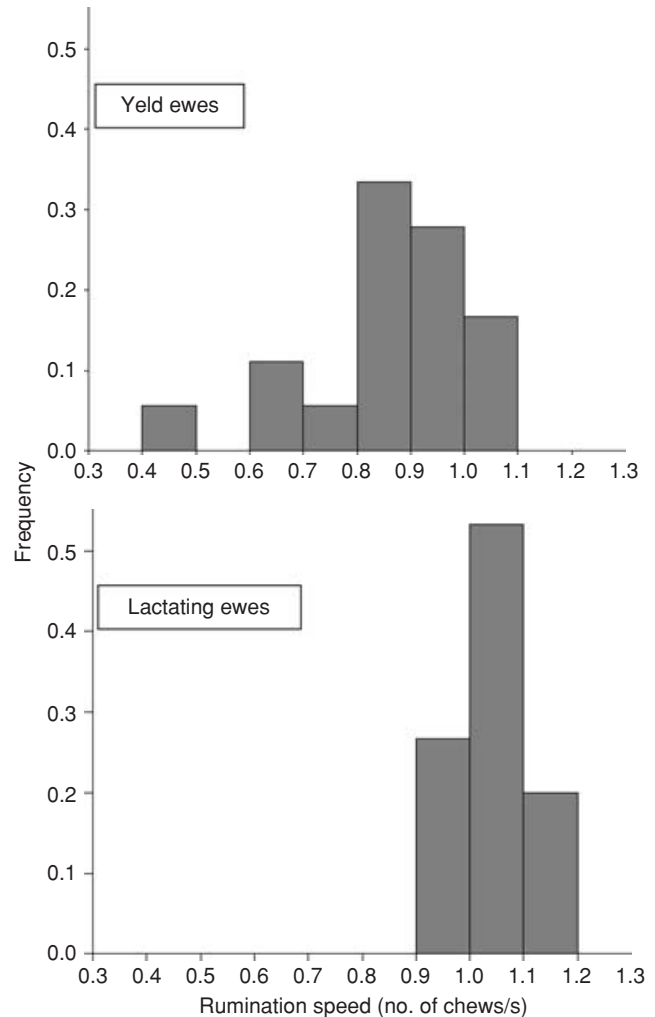
thereby reducing individual variation (Fig. 2). In contrast, yeld ewes, who ruminated more slowly, showed higher variance in rumination speed (Levene statistic$_{1,31} = 7.1$, $P = 0.01$; Fig. 2).

The difference in rumination patterns between lactating and yeld ewes occurred both before and after 1 September. The F test between the two nested models was significant, indicating that the slope was higher for lactating females compared to yeld ones, both before 1 September ($F_{1,17} = 8.62$, $P = 0.01$) and after 1 September ($F_{1,12} = 6.12$, $P = 0.03$).

DISCUSSION

To my knowledge, this is the first study to compare rumination behaviour to reproductive status in a free-ranging ungulate. My data clearly show that bighorn

ewes can adjust ruminating behaviour as a function of the presence/absence of offspring. Lactating ewes ruminated 1.21 times faster than yeld ewes and the variance in rumination speed was much greater for yeld ewes, reflecting more individual heterogeneity than in lactating ewes. Together, these results strongly suggest that the intensity of the selective pressures affecting a ewe's rumination patterns strongly differed according to whether she had to nurse a lamb or not; lactating ewes seemed to chew as fast as some physiological constraints allow them to, thereby reducing individual heterogeneity.

Rumination patterns could be affected by several individual characteristics such as tooth morphology (Pérez-Barbería & Gordon, 1998a,b), body weight (Pérez-Barbería & Gordon, 1998a) or age (Chadwick, 1983). There is no reason why lactating and yeld ewes should differ in dentition, however, and both groups of ewes had similar ages or body weights.

Several hypotheses can account for the increase in chewing effort during rumination by lactating females. Lactating ewes may have to ruminate more thoroughly to compensate for less time spent chewing while biting vegetation compared to other females. First, reducing the time spent chewing while grazing could allow increases in bite or vigilance (but see Illius & Fitzgibbon, 1994) rates. This probably does not hold for bighorn ewes, however, since in summer both bite and alert rates are the same for yeld and breeding ewes (Ruckstuhl & Festa-Bianchet, 1998). Similarly, reducing the time spent chewing while grazing could allow females with lambs to perform additional activities, such as lactation or grooming. Most of these activities (except possibly grooming), however, can be performed while chewing. Moreover, the time investment for such activities is probably small since lactating and yeld ewes have similar standing, grazing and walking time in summer (Ruckstuhl & Festa-Bianchet, 1998). The time spent standing (when most nursing and grooming take place) only represents about one-eighth of the total time budget (Ruckstuhl & Festa-Bianchet, 1998). The hypothesis that the increase in chewing speed during rumination compensates for less time spent ruminating per day can also be rejected, because lactating and yeld ewes have similar lying times (Ruckstuhl & Festa-Bianchet, 1998), and ewes seldom interact with their lamb when lying, so that the proportion of time spent ruminating when lying should be independent of reproductive status. The distance between the focal ewe and her lamb was estimated each time the lamb was visible: in three of 12 cases, the lamb was next to the mother, in five cases it was from 4.5 to 8 m away, and in four cases it was > 15 m away from its mother. Suckling and grooming usually occurred when a group finished ruminating and the ewes stood up.

Therefore, the increase in ruminating effort probably constitutes a way for lactating ewes to increase nutrient input (by ways other than an increase in bite rate or grazing time) rather than a way to compensate for temporal constraints imposed by the presence of the lamb. Because symbiotic micro-organisms in the rumen are inefficient in reducing particle size (Bjorndal et al., 1990;

Pérez-Barbería & Gordon, 1998a), the physical degradation of forage through chewing is vital to increase its surface area, increasing fermentation rate and reducing the lag to cell wall degradation (Reid et al., 1979; Pond et al., 1984). Domestic sheep chew faster than domestic goats during rumination, which may explain why sheep are more efficient in breaking down feed particles to less than 1 mm (Domingue, Dellow & Barry, 1991a), the threshold size for a high probability of leaving the rumen (Domingue, Dellow & Barry, 1991b). The main advantage of processing food more thoroughly is probably increased passage and ingestion rates, providing an alternative to increasing gut fill, reported for lactating Nubian ibex (Gross, Alkon & Demment, 1996) but unlikely in the case of bighorn sheep (Baker & Hobbs, 1987). Several parameters can affect intake rate. Neither foraging time nor bite rate differed according to ewe reproductive status in summer (Ruckstuhl & Festa-Bianchet, 1998). Bite size, however, was not measured. Bite size is mostly constrained by mouth size (Gordon, Illius & Milne, 1996) and forage characteristics (Illius & Gordon, 1987; Jiang & Hudson, 1994; Gibb et al., 1999). When total time available for grazing is restricted, however, sheep have been shown to maintain their instantaneous intake rate, mainly by increasing bite size (Iason et al., 1999), suggesting that animals still have flexibility (Shipley, Gross et al., 1994). Increased chewing investment is all the more important for lactating ewes in maintaining forage comminution efficiency comparable to that of yeld ewes since the greater amount of forage ingested is also probably of lower 'quality', for two reasons. First, every herbivore has to face a trade-off while grazing: if selecting large bites increases instantaneous intake rate, smaller bites allow the animal to be more selective and improve the quality of its diet (Shipley, Ilius et al., 1999). Thus, an increase in bite size (probably met by a deeper grazing) probably results in a mean diet of lower digestibility for lactating ewes (see also Jiang & Hudson, 1994). Second, except if lactating ewes chew more thoroughly every bite already while grazing, the mean ingested particle size would be expected to be larger given the larger bite size. Therefore, I propose that the increase chewing effort by lactating females during rumination is a way to 'defend' the digestion rate of more food with larger particle size of lower quality compared to yeld females (see also Kaske & Groth, 1997).

If lactating females do not increase ingestion rate compared to yeld ones, chewing more thoroughly while ruminating could increase forage digestion. Given the very high digestibility usually reported for forages commonly consumed (Robbins, 1983) however, this strategy would probably be insufficient to meet the high energetic requirements imposed by lactation and seems unlikely.

By increasing chewing rate while ruminating, lactating females may be able to avoid foraging longer than yeld females. Synchronization of activities is essential for group stability (Conradt, 1998; Ruckstuhl, 1998), therefore lactating females may ruminate as fast as possible to enjoy the benefits of being in a group (Oakes et al., 1992), without suffering from the costs of synchronization, such as reduced feeding time. High group

synchrony of activities is common in ungulates (Côté, Schaefer & Messier, 1997; Maier & White, 1998), and its benefits are thought to include enhanced predator detection or avoidance and foraging efficiency (Kie, 1999; Sevi, Casamassima & Muscio, 1999), all parameters of particular importance for lactating females. This reasoning assumes that lactating females adapt their foraging strategy to that of yeld females, but the opposite could be true: yeld females could forage longer when accompanied by lactating ewes, which could also allow them to benefit from the safety of being in a group. Sibbald & Kerr (1994) proposed that social facilitation of feeding behaviour could increase grazing time by fat ewes when accompanied by thin ewes. In the latter case, lactating bighorn ewes would both increase their feeding time and their digestion rate through rumination. It is likely that foraging behaviour of ewes will vary according to both reproductive status and group composition, and possibly be determined either by the proportion of lactating and of yeld ewes or by the reproductive status of dominant females if these tend to lead group activities. Given their different energetic requirements, one could expect lactating and yeld ewes to segregate, if they can form sufficiently large groups. Females with and without young tend to segregate in several ungulate species (Rutberg, 1984; Komers et al., 1993; Pérez-Barbería & Nores, 1994).

Ruckstuhl & Festa-Bianchet (1998) proposed that factors such as insect harassment or heat may prevent lactating ewes from increasing foraging time in summer. In this case, enhancing chewing effort while ruminating could be an alternative strategy to increase feeding efficiency. It would be interesting to repeat these observations later in autumn, when lactating females feed longer than yeld ones (Ruckstuhl & Festa-Bianchet, 1998), possibly also because predation pressure decreases as lambs become older. I would expect fewer differences in rumination patterns between ewes at that time of the year.

But why should yeld ewes not ruminate as fast as lactating ones? First, even if autumn body mass is positively correlated with winter survival, especially for old females (Festa-Bianchet, Jorgenson, Bérubé et al., 1997) there could be a locomotory cost to excessive accumulation of summer mass (Festa-Bianchet, Jorgenson, King et al., 1996). Second, mastication could increase tooth wear (Gross, Demment et al., 1995). Fitness consequences of the resulting loss of tooth effectiveness (Pérez-Barbería & Gordon, 1998a) can be very important (Leader-Williams, 1988; Skogland, 1988). Pérez-Barbería & Gordon (1998b) showed that red deer hinds with a low molar occlusal surface area had larger forage particles in their faeces. There is considerable individual variability in tooth wear at a given age in ungulates (Hewison et al., 1999). If the rumination patterns found in this study hold for other species, individual differences in reproductive effort (number of reproductive events for a given age as well as maybe litter size or offspring sex ratio) may partly explain individual variability in tooth wear within populations of wild ruminants, underlying a trade-off between reproduction and survival (Stearns, 1992).

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